MST 204.3

The Open University
Mathematics/Science/Technology
An Inter-faculty Second Level Course
MST204 Mathematical Models and Methods

mathematical models and methods

Unit 3

Animal populations: their growth and exploitation

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Animal populations: their growth and exploitation

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1.6

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Introduction

Twenty years ago, when I was a boy, kippers (smoked herrings) were a cheap meal. Now (1980), at around £1 per lb, they are hardly cheap, and are often difficult to obtain at all. In 1959, the North Sea herring stock was estimated to be 2.5 million tons; in 1975, to be 0.25 million tons. What happened? The answer is quite simple: herrings were being caught too fast, with the result that the size of the herring population fell. You may wonder why I say 'too fast' here. If any fish are caught, and hence removed from the population, surely the population will consequently be reduced? This simple argument falls down, because populations replenish themselves—by reproduction. Fishing will not necessarily cause a population to be reduced in size, so long as no more fish are caught than can be replaced by births. The problem with North Sea herring is that *too many* fish have been caught; fish have been removed at a greater rate than that at which the population is able to replace them.

The North Sea herring population is by no means an isolated example of the effect that human exploitation can have. A dramatic example is provided by the Passenger Pigeon, a species that was common in North America when European colonists arrived, and which was heavily exploited for food. This species may have been the most numerous bird the world has ever seen, with individual flocks in the early nineteenth century being estimated in the thousands of millions. A hundred years later (by 1914) the species was extinct, and hunting seems to have been the major cause of this. The Great Auk, a North Atlantic seabird much exploited by sailors for fresh meat, is another species whose extinction is attributable to human overexploitation, and many other examples could be quoted.

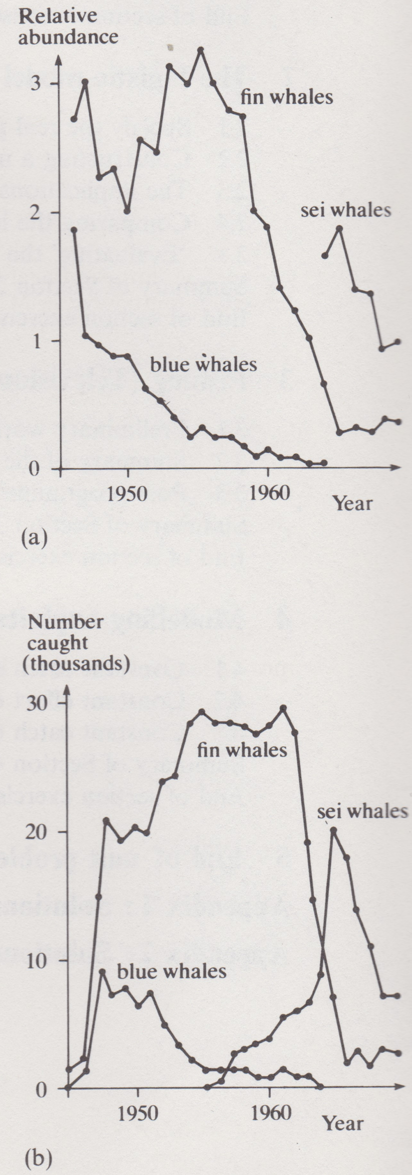


Figure 1. The effect of fishing on the populations of various Antarctic whale species since 1945. (a) Estimates of variations in the abundance of various species (b) Catches of these species.

These examples show that where animal populations are much reduced by hunting the possibility of extinction must be taken seriously. The biology of fish species is such that they are less likely than mammals or birds to suffer total extinction, but even so the reduction of population levels such as has occurred with North Sea herring is of considerable commercial significance. The fishery-induced reduction in the numbers of various whale species (see Figure 1) is of both commercial and ecological concern, for they are mammals for which the possibility of extinction is real.

Uncontrolled exploitation (hunting or fishing) may kill the goose that is laying the golden eggs, or at least maim it severely. To avoid this, some control of levels of exploitation is clearly required. But what degree of control? How much fishing for herring should be allowed? How many Great Auks could have been taken without exterminating the population?

Clearly if no herrings are caught then the population will not be reduced, but there would be no kippers! On the other hand, if fish are taken too fast, the population is reduced, and may eventually be exterminated, with the same end result (no kippers). Is there, somewhere between these extremes, a sensible compromise? If so, how does one determine it? There is, and it can be determined, in part at least, by setting up a mathematical description of the problem, as you will see later in the unit.

It is unlikely to be a surprise to you to hear that mathematics is a useful tool in solving problems in the real world. It may be a surprise to see the context in which I am suggesting its application here. One aim of this course is to familiarize you with the use of mathematics, not only in the traditional area of physical science, but also in other fields such as biology and management.

In applications of mathematics to fields such as these, it is not usually possible to achieve the same accuracy of agreement between the predictions of the mathematics and the real situation that one can in areas of physics, for example. For this reason it is particularly important to maintain here an awareness of the *relation* between mathematics and the reality it is being used to describe. One needs to keep in mind such factors as the degree of accuracy with which the mathematics corresponds to reality, noting those situations in which the correspondence is good and those in which it is bad. One needs to do this in order to be realistic about the value of the conclusions of one's mathematical manipulations.

The use of mathematics in solving real-world problems is often referred to as **mathematical modelling**. This might be defined as the process of describing a real-world situation with mathematics, in a way suitable to assist in the solution of the given problem. It is of some value to emphasize the idea of 'modelling' as this acts as a reminder that there are things other than the mathematics itself to be borne in mind when using it. The flowchart of Figure 2 shows the various activities involved in modelling.

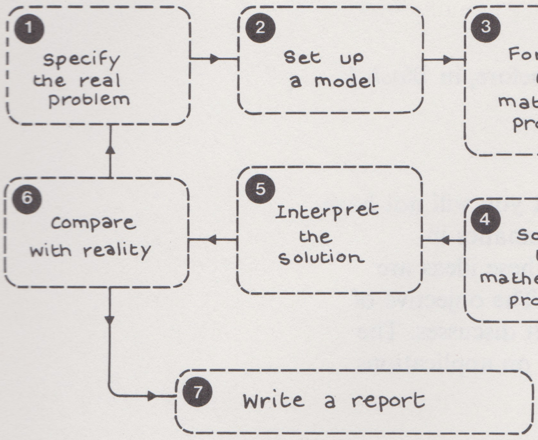


Figure 2. A flow-chart analysing the process of mathematical modelling (introduced in *M101, Block V*)

The diagram is there to help, both when constructing a model yourself, and when critically examining a description of an application of mathematics. However, it is not always possible to determine exactly in which 'box' of the cycle a particular activity falls, nor is modelling always conducted in quite so logical an order as to pursue a route from Box 1 through to Box 6, then back to the beginning. The diagram is not a straitjacket, but provides suggestions as to the sort of things that you should do when modelling, and shows their logical order.

The underlying aim of this unit is to teach you something about modelling. This is more effectively done by looking at a particular example than by talking about the process of modelling in general. However, I will take the opportunity in the text of making some general points in the context of our example.

This unit may be regarded as a 'case study' of mathematical modelling. As such it is concerned with models in one particular area, that of populations; and for one particular purpose, to investigate the effect of exploitation on a population. You should not be surprised to find that the unit contains a good deal of information about, and discussion of, populations. Mathematical modelling is not just a matter of mathematical manipulation. To construct or to evaluate a model one needs detailed information about the real situation being discussed.

Study guide

In order to set up a model to investigate the effect of exploitation on the numbers in a naturally occurring population I will proceed in two stages. First I will investigate the way natural populations vary when *not* exposed to human exploitation. Having found a model of this that corresponds adequately with observed data, I will then develop the model to take into account exploitation of the population.

The first two sections of the unit are mainly concerned with the variation in numbers in an unexploited population. The first section looks at some simple models for this, with some discussion of the general strategy of modelling. The second section concentrates on developing an adequate model of an unexploited population in a state of increase. A model taking exploitation into account is discussed in Section 4. The television programme looks briefly at the practical problems of using models in fisheries management. The programme is summarized

in Section 3 but can be viewed prior to your study of the earlier parts of the unit, if necessary. Section 5 contains some problems which, in developing ideas from the rest of the unit, provide an opportunity for you to do some modelling for yourself.

You will probably find that Section 2 requires slightly more study time than the other sections of the unit, whereas Section 3 requires slightly less study time.

If you have not finished Sections 1 and 2 when the television programme is due to be broadcast, make sure you have read the preliminary notes at the beginning of Section 3 before watching the programme.

To M101 students

You will find that you have met some of the ideas in Section 1 before, in *Block V* of *M101*. I hope you will find the revision useful.

To MS283 students

In this unit we will introduce certain ideas covered in *M101* that you will not have met before. These concern the process of *modelling*—using mathematics in describing and solving real-world problems. You may find that these ideas are introduced rather abruptly here. Don't worry if that is the case. The objective of this unit is that you learn about the specific population models it discusses. The general modelling ideas will take shape as you study more units on applications later in the course.

To TM281 students

This is the first unit of *MST204* in which modelling is discussed. This is a subject that you spent time on in *TM281*. The topic of modelling is also discussed at some length in *M101*, and although the basic messages are the same in the two courses, there are some differences in the way they are presented. In the early part of this unit I will introduce certain general ideas about modelling in the style in which they appear in *M101*. So the form in which these ideas appear will be new to you, though I hope you will see that the underlying message is the same.

1 The exponential model

1.1 Some examples of population change

Our first task in this unit is to investigate the way in which numbers in unexploited populations vary with time. We will look for mathematical models to assist in this investigation. When setting up a mathematical model, it is important at the outset to be as clear as possible about the *purpose* of the model. It can help to clarify this if you can decide how the success or otherwise of your model will be judged in the end. What are the criteria here for a good model?

purpose of model

criteria for success

Surely in this case a good model is one whose implications correspond well with the way real populations are observed to vary with time. So to test such a model we will need further information about real-world populations. Further, in this instance at least, a natural place to start the modelling process might be to examine such real-world data for revealing patterns.

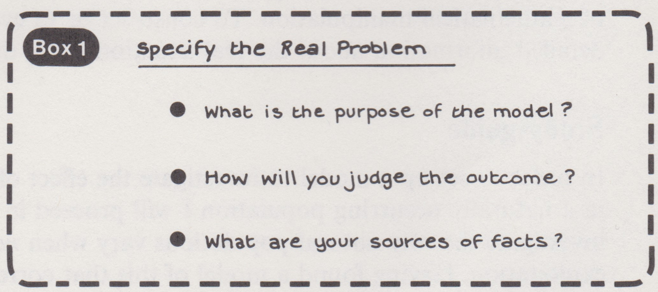


Figure 1. Box 1 of the 'seven-box diagram' shown in Figure 2 of the introduction.

Figures 2(a)–(n) on the next two pages show data on a number of populations. I have deliberately chosen diverse examples: populations of different types of animal and populations showing different types of variation. I have not considered plant populations, and I have only given examples where the population numbers are not significantly affected by human exploitation.

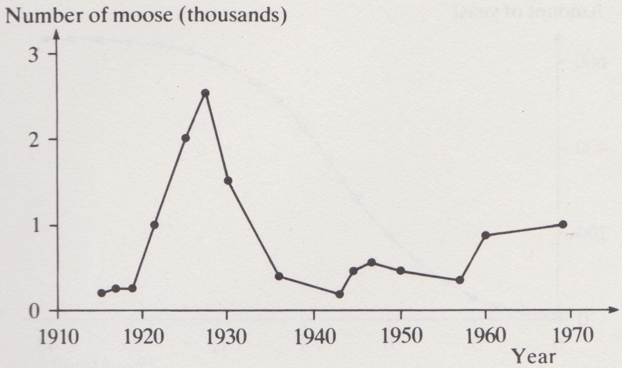


Figure 2(a). Estimates of the population of moose on Isle Royale in Lake Michigan. (Moose arrived on the island in about 1910.)

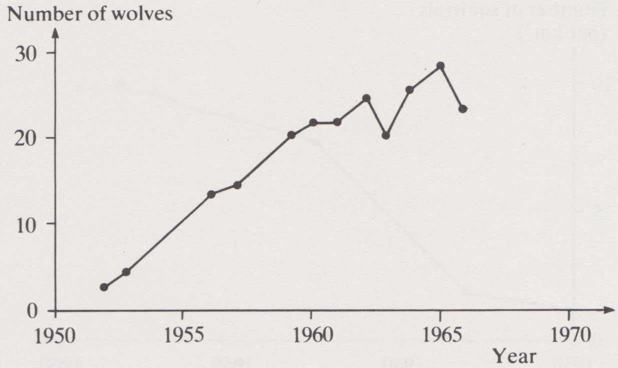


Figure 2(b). Estimates of the number of wolves on Isle Royale. (Wolves arrived on the island in about 1948.)

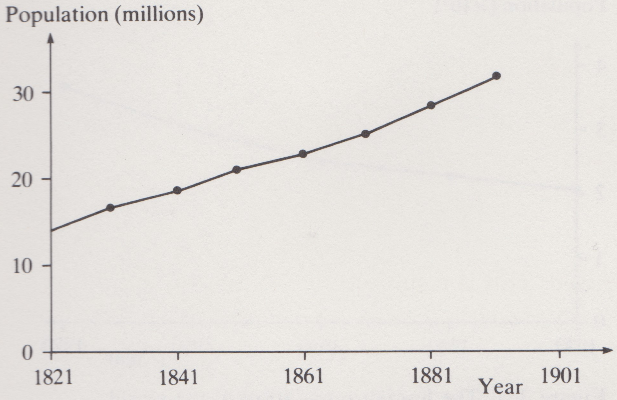


Figure 2(c). The human population of Great Britain (1821–1891), taken to the nearest half million.

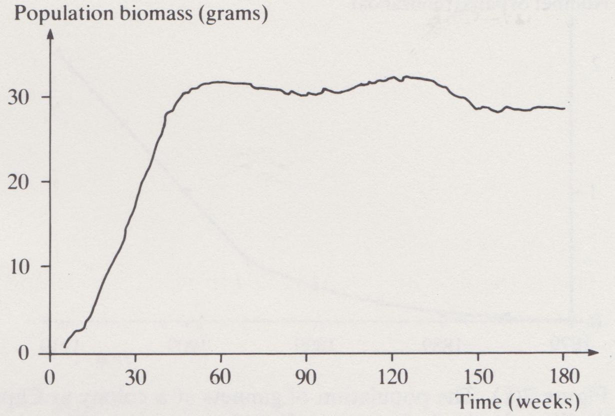


Figure 2(d). The growth of a population of guppies in a laboratory aquarium (after Sulliman and Gutsell, 1958).

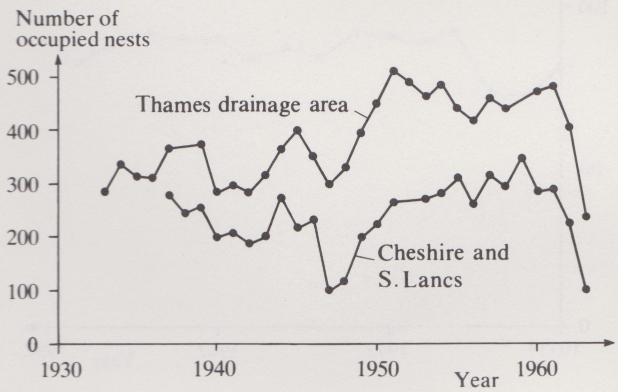


Figure 2(e). Number of breeding pairs of heron (*Ardea cinerea*) in two parts of England (1933–1963). Data from British Trust for Ornithology, analysed by J. Stafford (after Lack, 1966).

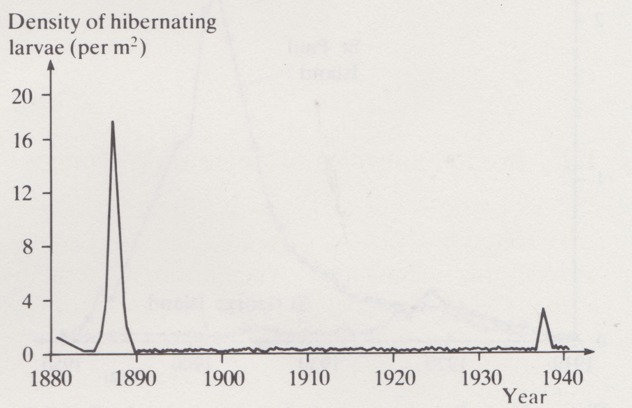


Figure 2(f). The population density of a moth (*Dendrolimus*) in a forest at Letzlinger, Germany.

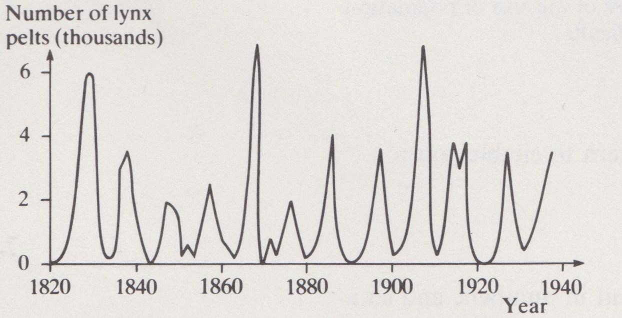


Figure 2(g). Variations in the population of lynx in the Hudson Bay area of Canada, estimated from the number of pelts sold to a company each year.

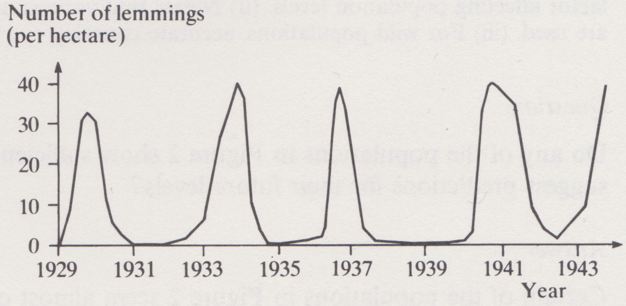


Figure 2(h). The population density of lemmings in the area near Churchill, Canada.

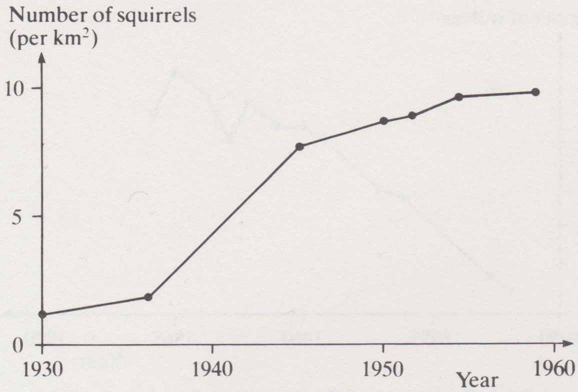


Figure 2(i). The population density of the grey squirrel at selected sites in Great Britain.

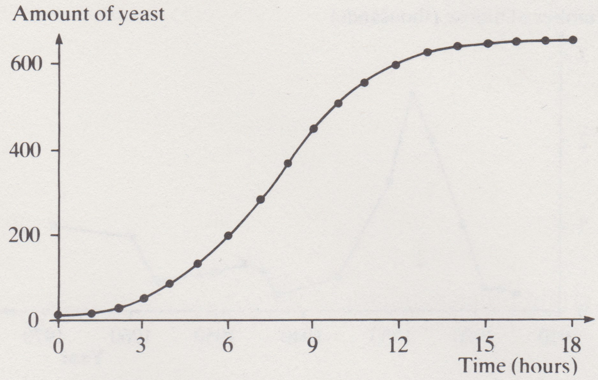


Figure 2(j). Growth of a laboratory culture of yeast cells. Data from Carlson 1913 (after Pearl, 1927).

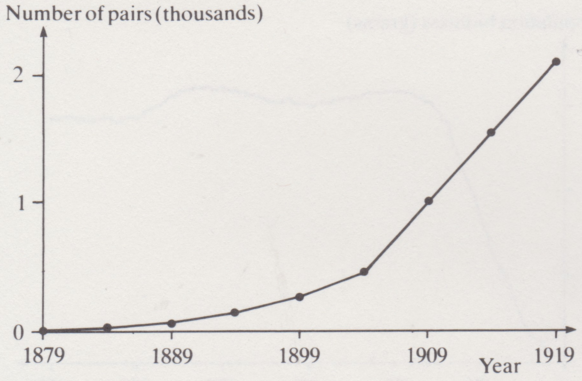


Figure 2(k). The population of gannets at a colony at Cape St. Mary in the St. Lawrence, Canada.

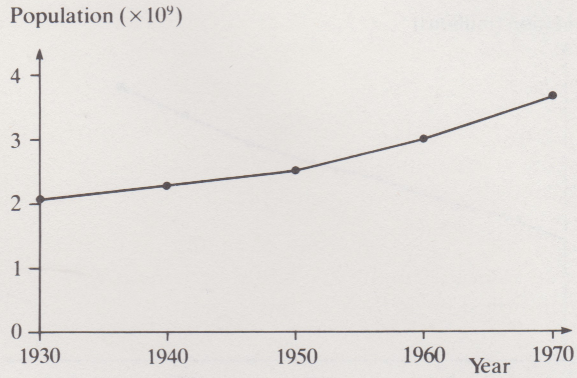


Figure 2(l). The human population of the world (1930–1970).

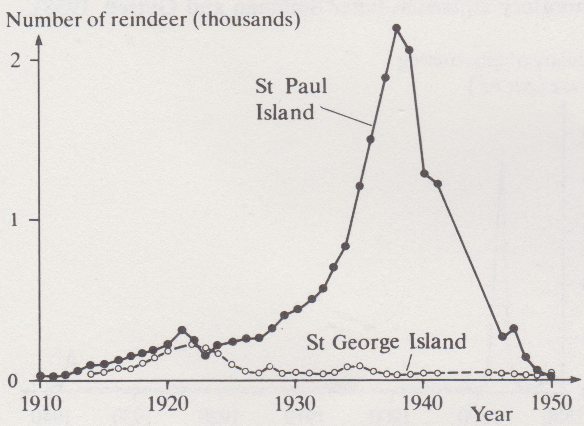


Figure 2(m). Reindeer population on two of the Pribilof Islands in the Bering Sea, from 1911, when they were introduced, until 1950. (After Scheffer, 1951).

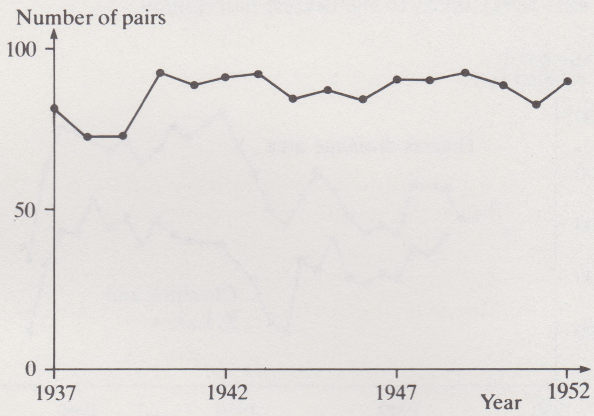


Figure 2(n). Population of the yellow-eyed penguin (*Megadyptes antipodes*) in Dunedin, New Zealand.

Notes: (i) In none of these examples is human exploitation believed to be a significant factor affecting population levels. (ii) Notice that various measures of the size of population are used. (iii) For wild populations, accurate counting can be difficult.

Question

Do any of the populations in Figure 2 show sufficient pattern to enable you to suggest predictions for their future levels?

Answer

Certain of the populations in Figure 2 seem almost constant in numbers, and so a reasonable prediction of future levels would seem to be that they will stay constant. For example, the wolf population of Figure 2(b) was growing, but has now apparently stabilized. Its average size in 1962–1966 was about 24. One might

therefore predict the population to stay constant at 24. More reasonably, one might predict it to lie in the range 24 ± 4, giving an indication of the extent of uncertainty in the prediction.

Similarly, the penguins of Figure 2(n) seem likely to remain in the range 85 ± 11 and the populations in Figures 2(d), 2(i) and 2(j) seem likely to remain in similarly restricted ranges. Despite its earlier variability, the moose population of Figure 2(a) also now seems fairly stable, and presumably might be expected to stay that way unless conditions change.

Certain other populations show a degree of pattern that suggest *qualitative* predictions of the way they will vary, but *quantitative* estimates are not so easy.

The lynx population in Figure 2(g) shows a regular pattern of increase and decrease, with low levels of population every 10 years (when the population is in the hundreds) and high levels between when it is in the thousands. It seems reasonable to predict that this *pattern* of variation will continue, but to predict the size of the population in a given year would be difficult to do with confidence (on the basis of a simple examination of the data, anyway). Similar comments apply to the lemming population of Figure 2(h).

The populations in Figures 2(k) and 2(l) may be expected to continue to increase rapidly in the immediate future. (Although the example in Figure 2(m) shows the dangers inherent even in this prediction.)

The human population data of Figure 2(c) appear to lie close to a straight line. Fitting such a straight line could provide a way of predicting the size of this population. Let us look at this now.

1.2 Linear extrapolation: empiricism

A straight line which gives a fairly good fit to the data in Figure 2(c) is

$$P = 13.4 + 0.27t \tag{1}$$

where P is the population in millions at a time t years after 1821. (Measuring population in millions, and time from 1821 rather than from 0 AD, leads to a simpler equation.)

Had I lived in 1891, I might have set up Equation (1) to predict future population levels. Using this model, I would have predicted a population in 1971 of 53.9 million. In fact the population in that year was 53.8 million. So Equation (1) provides a possible method of predicting population levels that seems to give fairly accurate results. It might seem so simple that there is nothing more to be said about it. However there are a few points I would like to make.

Observe that the first step in setting up the model is to choose suitable variables. That seems straightforward enough here: we are interested in the variation of population with time. Even so, it is necessary to define the variables clearly. 'P is the population at time t' would not be sufficient; to relate the model to the data it is essential to specify the time origin, and the units in which the variables are measured.

choose and define variables

specify units

A more subtle point: in choosing to quantify population as 'number of individuals in the population', differences between individuals are ignored. This is a natural approach, but it is not the only one. For example, the variation in size amongst individual fish in a population is sufficient to make 'total mass of the population' a measure of population size significantly different from 'number of fish', and the former measure is in fact preferable in the context of fisheries models.

Having defined the variables, I looked for a relationship between the variables. Having found one, I took the opportunity to check its predictions against known information.

look for relations

The procedure used here to find the relation between P and t—Equation (1)—may be labelled **empiricism**, the examination of known data for pattern. Having found an empirical relation, I **extrapolated**; that is, used the relation to predict P for values of t outside the range of values of t for which information was given initially. Here extrapolation provided a fairly accurate result, but this was remarkably lucky. Let us see why.

Question

Figure 3 shows data on a variable z at time t years from 1821.

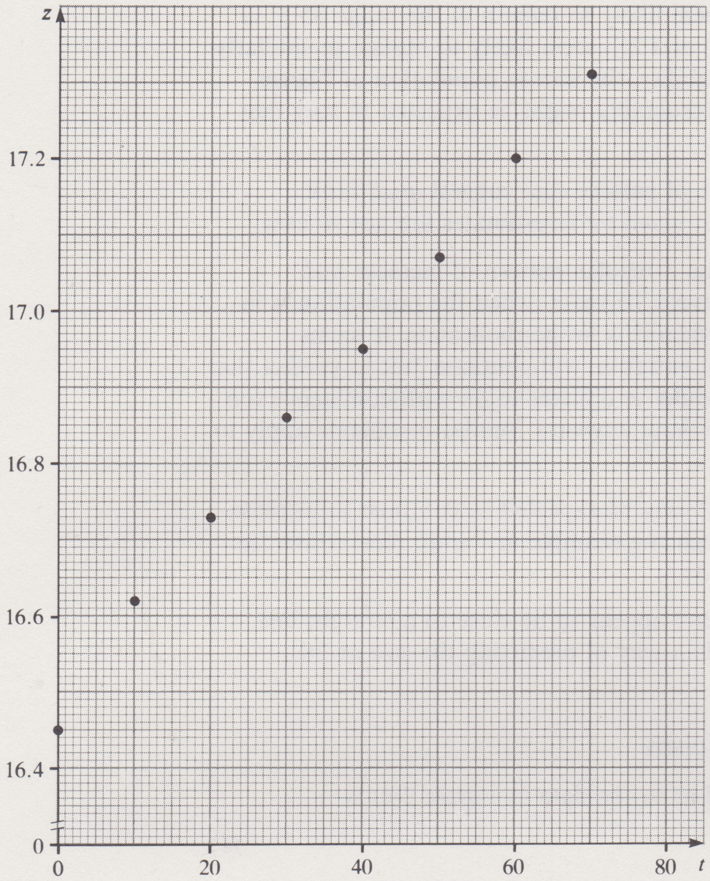


Figure 3. Data on a variable z at various times t where t is the number of years since 1821.

The method of least squares was introduced in *M101*, but not in *TM281*. It is a way of choosing a straight line to fit given data well (similar to that in *TM281*, *Unit 16*, subsection 2.2).

Can you find an empirical relation between z and t? (A reasonable fit will do; there is no necessity to calculate the best straight line by least squares.) What does this predict as the value of z in 1971?

Answer

Actually, the variable z in the question is not a completely new one; it is the natural logarithm of the population numbers from Figure 2(c) that we were discussing before. The empirical approach also suggests a linear relationship between z and t

$$z = 16.50 + 0.0118t.$$

You may have found a slightly different equation

But $z = \log_e (P \times 10^6)$ (remember that P was the population in millions), so this equation can be rewritten as

$$\log_e (P \times 10^6) = 16.50 + 0.0118t.$$

Now $\log_e (P \times 10^6) = \log_e (P) + \log_e (10^6) = \log_e P + 13.82$, so this equation is equivalent to

$$\log_e P = 2.68 + 0.0118t$$

or

$$\begin{aligned} P &= e^{2.68} \times e^{0.0118t} \\ &= 14.6 \times e^{0.0118t}. \end{aligned} \qquad (2)$$

Here, by adopting a different (but still empirical) approach, I have arrived at a very different equation relating P and t. There is just no way of telling, simply by examining the given data for 1821–1891, which, if either, of Equations (1) and (2) is preferable. In fact, in this example I have an additional piece of data against which I can test the models. I know that the population in 1971 was 53.8 millions. Equation (2) predicts a population in 1971 of about 86 millions—a much less accurate estimate than that given by Equation (1).

Equations (1) and (2) give similar values for P if t is small, which is why both fit the data for the period 1821–1891 well, but they give very different results if t is large. This shows that it is inadvisable to extrapolate very far from the given range of data when adopting this empirical approach. If the only reason one has for believing in a formula is that it fits the data over some limited range of times one can have little confidence in such a formula for times far outside this range, partly because errors build up rapidly as the range of extrapolation is increased and partly because this empirical method gives no understanding of *how* the system works so that one has no way of telling whether it will go on behaving in the future as it has in the past.

Dangers of extrapolation

1.3 An attempt at theory: exponential change

In our first attempt at modelling population change, we examined population data for pattern. What we did not do is give any thought to the actual processes that cause populations to change and we were therefore unable to build such considerations into our model. If we construct a model based on consideration of the real situation, and the implications of the model correspond well with real data, then there will be reason to feel more confident in the predictions of the model than with simple extrapolation.

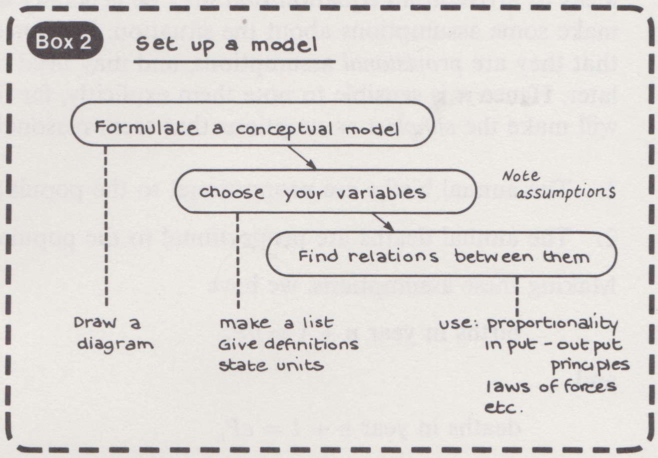


Figure 4. Box 2 of the seven-box diagram.

Why do the numbers in a population change? The obvious reasons are that individuals are born and individuals die. This suggests the equation

$$\begin{pmatrix}\text{Increase in population}\\ \text{during a period of time}\end{pmatrix} = \begin{pmatrix}\text{Births during}\\ \text{the period}\end{pmatrix} - \begin{pmatrix}\text{Deaths during}\\ \text{the period}\end{pmatrix}. \qquad (3)$$

This is an example of a principle that is frequently useful in suggesting relations between variables.

Increase = Input − Output.

We refer to this as the **input–output principle**. Notice that you must be prepared to interpret a negative increase as a decrease (when output exceeds input).

Question

Does Equation (3) cover all possible inputs and outputs to a population?

Answer

One possible output is fishing, or removals from the population by other forms of exploitation, but it is reasonable to regard such output as coming under the heading of 'deaths'. The movement of populations in space will cause inputs and outputs to particular populations, not covered by births and deaths. To cover these we should modify Equation (3) as follows:

$$\text{Increase in population} = (\text{Births} + \text{Immigration}) - (\text{Deaths} + \text{Emigration}) \qquad (4)$$

This is a general equation describing population change, and will simplify to Equation (3) if there is no migration.

To proceed further, we must translate these ideas into mathematical relations. We shall see that the input–output principle leads naturally to mathematical relations either in the form of *recurrence relations* or of *differential equations*. I will concentrate first on the formulation in terms of recurrence relations.

Suppose that P_n denotes the size of a population n years after some specified time origin. Then the increase in the population in year $n+1$ is $P_{n+1} - P_n$.

To arrive at an equation that we have any chance of solving we need to express the right-hand side of Equation (4) in terms of the variables *population* and *time*. It is sensible first to consider the situation where there is no migration or exploitation. If we can solve this simpler problem first, we can return to the more complicated one later. In this case, Equation (4) becomes

$$P_{n+1} - P_n = (\text{Births in year } n+1) - (\text{Deaths in year } n+1) \tag{5}$$

Model now assumes no migration or exploitation

How can births and deaths be expressed in terms of population and/or time? For a particular population one might return to the empirical approach here, and examine data on births and deaths. However, I want, if possible, to use general ideas to arrive at an equation that may be generally applicable. To do this I will make some assumptions about the situation. I will make these in the consciousness that they are *provisional* assumptions, and may need modification or rejection later. Hence it is sensible to note them explicitly, for future reference. As a start, I will make the *simplest* assumptions that seem reasonable, which are:

To start: make assumptions; note them explicitly; be simple.

1. The annual births are proportional to the population at the start of the year;
2. The annual deaths are proportional to the population at the start of the year.

Provisional assumptions about births and deaths

Making these assumptions, we have

$$\text{births in year } n+1 = bP_n$$

and

$$\text{deaths in year } n+1 = cP_n$$

Formulate the mathematical problem (Box 3 of the seven-box diagram).

where b and c are constants. Hence Equation (5) becomes

$$P_{n+1} - P_n = bP_n - cP_n = (b-c)P_n. \tag{6}$$

Equation (6) is a recurrence relation of a type covered in *Unit 1*, Section 1. To solve it, rewrite Equation (6) as

$$P_{n+1} = (1+b-c)P_n.$$

The solution of this is

$$P_n = (1+b-c)^n P_0. \tag{7}$$

Solve the mathematical problem (Box 4).

Because this equation is of the form $P_n = A \times B^n$ (for $n = 1, 2, 3 \ldots$) where A and B are constants, I will call the model constructed above the **exponential model.** We now have an equation giving the population in terms of time. Arguably, the modelling problem is solved. But is it?

Exercise 1

In January 1960 a rabbit colony had 100 members. Observations on the colony during the past year suggest that in each three month period the average breeding success of a female rabbit is 2 young reared to maturity, while, during each period, 50% of the population at the start of the period die. Use assumptions of the type made above to find an equation describing the variation of the population with time. Note the assumptions you make in setting up the equation. How realistic do you think its predictions are?

[*Solution on p. 45*]

1.4 Interpret the solution

Exercise 1 illustrates one strikingly unsatisfactory general feature about the solution arrived at in Equation (7). If $b > c$ the population is predicted to continue to grow without any limit to its size (see Figure 5(a)). This is surely unrealistic. Rabbits may breed like rabbits, and their populations may undergo dramatic increases in numbers, but these increases never continue indefinitely. For the example in Exercise 1 the model predicts for the year 2000 a rabbit population of

$$100 \times \left(\frac{3}{2}\right)^{160} \simeq 10^{30}.$$

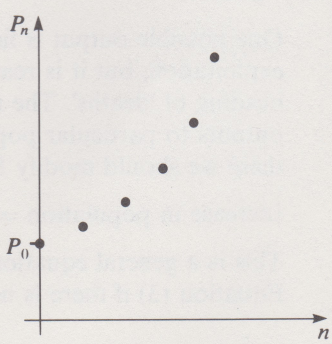


Figure 5(a). Sketch graph of $P_n = (1+b-c)^n P_0$ ($n = 1, 2, \ldots$) when $b > c$.

If the colony covered the whole of Australia, this would give a population density of the order of 10^{17} rabbits *per square yard*. Even in Australia, rabbit populations rarely become this dense.

A whole heap of hot cross bunnies.

The general character of the implications of the model is quite different if b is not greater than c. If b is less than c, the population declines gradually towards zero (see Figure 5(b)). Populations do decline in certain circumstances, and there is no immediately obvious reason why they should not decline exponentially. However, there is one implication here that we can see immediately is unrealistic. Equation (7) never actually predicts a zero population; rather it predicts one that approaches zero as a limit, but never actually takes that value.

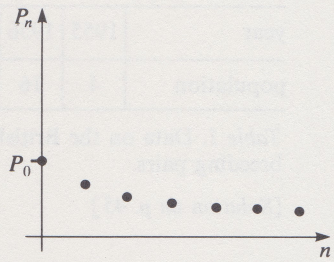


Figure 5(b). Sketch graph of $P_n = (1 + b - c)^n P_0$ ($n = 1, 2, \ldots$) when $b < c$.

Question

Why is this unrealistic? Can you see what went into the setting up of the model that lead to this unrealistic feature?

Answer

Eventually the model will predict populations such as 'half a rabbit', which are evidently meaningless. The population cannot 'tend' to zero, as implied by the mathematics; it must either stabilize at a non-zero level, or become extinct (or possibly rise again). The problem here is that we have modelled 'population' as a variable that may take *all real* values; in actuality it can only take *positive integer* values. (The model also predicts fractional rabbits for $b > c$, though I did not comment on this point before.)

The implications of Equation (6) are again different in character when b actually equals c. The population is now predicted to be precisely constant. This may look the least realistic of the three cases. It is however probably the best reflection of reality for many populations. We saw examples in Figure 2 of populations that, although not constant, do fluctuate within a limited range. For such populations, births and deaths are equal on average, but usually out of balance in any given year.

So far we have only compared the general features of the behaviour of Equation (7) with reality. To *validate* a model we need to check that the behaviour implied by the model fits real data, at least sufficiently accurately for the purpose of the model.

Question

How can we compare Equation (7) with data? Taking a hint from Figure 6, is there a graph that should be straight?

Answer

There is. Take natural logarithms of

$$P_n = (1 + b - c)^n P_0$$

to give

$$\log_e P_n = n \log_e (1 + b - c) + \log_e P_0.$$

Now $\log_e(1 + b - c)$ and $\log_e P_0$ are constants, so if we plot the logarithm of population $\log_e P_n$ against time n the graph obtained should be linear.

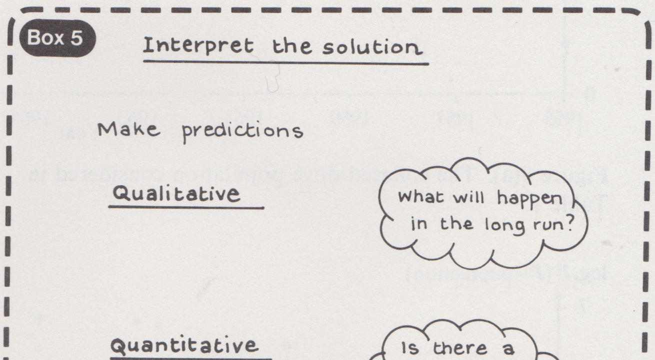


Figure 6

Exercise 2

Table 1 gives data on a real population. Does this fit an exponential model? Can you arrive at an equation fitting this data?

To test if data is exponential—take logs.

year	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
population	4	16	45	100	205	675	1900	4650	10200	18855

Table 1. Data on the British population of collared doves, estimated as the number of breeding pairs.

[*Solution on p. 45*]

1.5 Compare with reality

In Exercise 2 you compared the behaviour implied by the model with one example of real data. There is by no means an exact agreement between model and data (see Figure 8(a)), but there is a degree of agreement. To draw conclusions we really need to examine more than one set of data. In Figure 8 the logarithms of data for several of the examples in Figure 1 are plotted.

Box 6 Compare with reality

VALIDATE

Do the predictions agree with the data?

EVALUATE

Does the model fulfil its purpose?

ITERATE

Can the model be improved?

Figure 7

Question

Comment briefly on the relationship of the exponential model to the various data in Figures 8(a)–(f) below and on the next page.

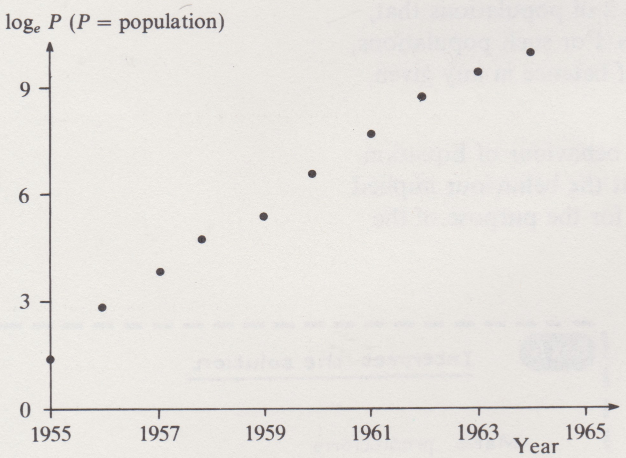


Figure 8(a). The collared dove population considered in Table 1.

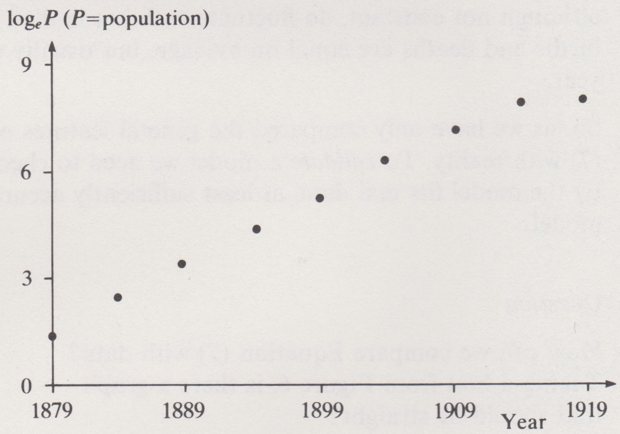


Figure 8(b). The gannet population plotted in Figure 2(k).

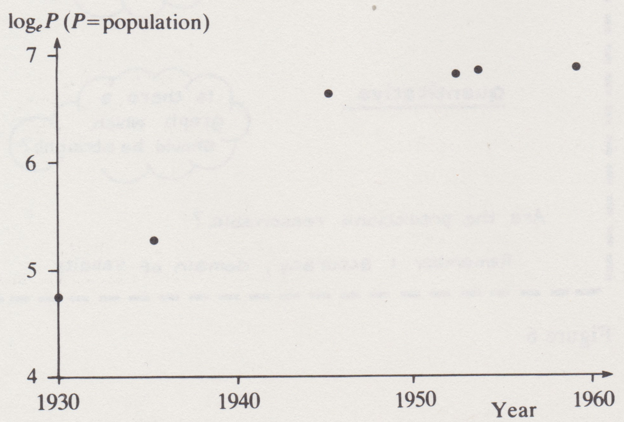


Figure 8(c). The squirrel population plotted in Figure 2(i).

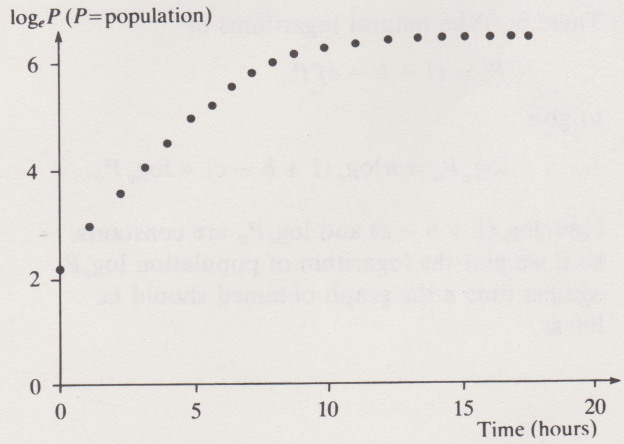


Figure 8(d). The yeast population plotted in Figure 2(j).

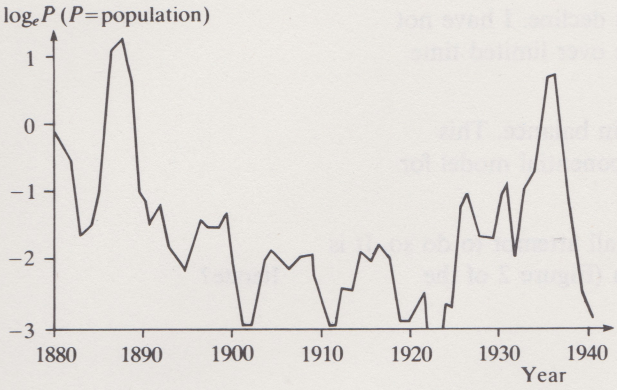


Figure 8(e). The moth population plotted in Figure 2(f).

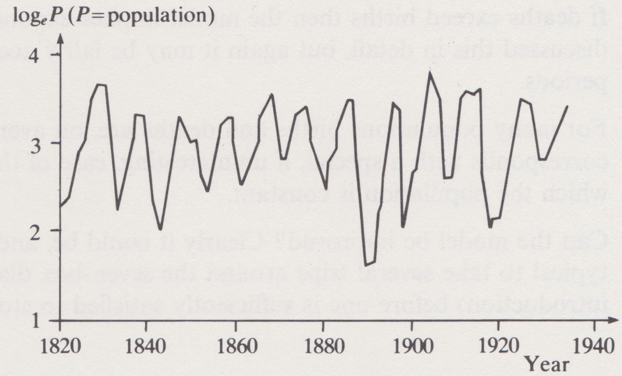


Figure 8(f). The lynx population plotted in Figure 2(g).

The graphs are plots of the logarithms of various population data: (a) the data on collared doves considered in Exercise 2; (b)–(f) the data for some of the populations for which the 'raw data' was plotted in Figure 2.

Answer

Compare the model with data.

We observe that the exponential model fits the data in Figure 8(a) and (b) fairly well. In (d) the exponential model fits part of the data well—that for the first few hours. The early data in (c) is sparse, but could fit the model fairly well, also. During each period of rise or fall of the lynx population (f) the population variation is approximately exponential. So in (c), (d) and (f) the exponential model gives a picture of the population variation for *part* of the time period for which data is available, but taken as a whole would give a very misleading picture. Finally, the insect population in (e) varies very greatly, but not in a way that corresponds at all with the exponential model.

Having constructed a model, and found that it fails to correspond to reality, at least in some circumstances, one should consider *why* this is the case.

Think about it.

Exercise 3

(i) What assumptions were made in setting up the exponential model? Give examples of real factors they do not take into account.

(ii) Suggest reasons for:

(a) the divergence from exponential growth of the populations in Figures 8(c) and 8(d),
(b) the total lack of exponential variation of the population in Figure 8(e).

[*Solution on p. 45*]

Evaluate

Domain of validity

Accuracy

The exponential model has three cases: population increase, population decrease, and constant population. Our main interest is in population increase and I will discuss this case first. We have seen examples of data that correspond fairly well with the model (Figures 8(a) and 8(b)) and other examples where *part* of the available data corresponds with the model. We have noted that the long-term behaviour implied by the model (unlimited population increase) is not reasonable and cannot be sustained (see Figures 8(c) and 8(d)). The model can only give sensible results if we restrict its domain of validity to finite (usually short) periods of time. Even over restricted time periods, the model is not entirely accurate; one must decide whether it is *sufficiently* accurate for one's purpose. I set out to look for a model to describe and predict the variations of an unexploited population with time. It is not possible to state unequivocally whether or not the model is 'sufficiently accurate' for this purpose. In this instance I have thrown a very wide net in stating my purpose; with a more specific task in mind I would expect to be able to give a less equivocal answer on this question of accuracy, although this is always going to be a matter of judgement.

Note that I am discussing exponential growth *as a model of populations.* Exponential growth may be an extremely accurate model of other phenomena.

In summary, if we set up a model on the assumptions that the birth and death rates are proportional to the population, and births exceed deaths, we obtain a model implying exponential growth. For some populations, and for limited periods of time, exponential growth is a fairly accurate model.

If deaths exceed births then the model implies exponential decline. I have not discussed this in detail, but again it may be fairly accurate over limited time periods.

For many populations births and deaths are, on average, in balance. This corresponds with a special, if uninteresting, case of the exponential model for which the population is constant.

Can the model be improved? Clearly it could be, and I shall attempt to do so. It is typical to take several trips around the seven-box diagram (Figure 2 of the introduction) before one is sufficiently satisfied to stop.

Iterate?

1.6 Formulation in terms of a differential equation

Before I make any substantial modifications to the model, I should like to look briefly at an alternative mathematical formulation, based on very similar assumptions to the model just discussed.

This time we represent the population $P(t)$ as a continuously varying function of time t. Again consider the situation in which there is no migration or exploitation, and make the same basic assumptions as before: that births and deaths in a short time period are proportional to the population at the beginning of the time period. Assume also that births and deaths are proportional to the duration of the time period.

I shall use the input–output principle to set up a differential equation. Consider a short period of time of duration h, starting at t. During this period:

$$\begin{aligned}&\text{increase in population} = P(t+h) - P(t)\\&\text{input to population} = \text{births} = BP(t)h\\&\text{output from population} = \text{deaths} = CP(t)h\end{aligned}$$

where B and C are constants. Hence

$$\begin{aligned}P(t+h) - P(t) &= BP(t)h - CP(t)h\\&= (B - C)hP(t).\end{aligned}$$

Rearranging gives

$$\frac{P(t+h) - P(t)}{h} = (B - C)P(t).$$

This equation holds for all small values of h, and so we can let h tend to zero. In the limit we have

$$\frac{dP(t)}{dt} = (B - C)P(t). \qquad (8)$$

A differential equation model

An argument of this form is often useful in setting up differential equation models.

Exercise 4

(i) Go through boxes 4–6 of the modelling cycle (see Figure 2 of the introduction) for this differential equation model.

(ii) Comment (briefly) on the relationship between the assumptions made in this model, and those made in the recurrence relation version. Are there circumstances in which either seems more appropriate?

[*Solution on p. 45*]

In this case, the implications of a differential equation model are essentially the same as those of the recurrence relation model constructed earlier. (In more complicated models the implications of apparently similar differential equation and recurrence relation formulations would often not be the same, though.)

Summary of Section 1

One method of modelling population changes is **empiricism**; that is, fitting some simple equation such as a straight line to the data. However, the use of this method for prediction amounts to **extrapolating** from the data, a notoriously inaccurate procedure. A more reliable method of modelling is to use the **input–output principle**:

increase = input − output

to set up a recurrence relation or differential equation. If both input (births) and output (deaths) are assumed proportional to the population P, then this model predicts an exponential growth or decay of the population. It is therefore called the exponential model. The model has many weaknesses, but for some populations, and for limited periods of time, the graph of $\log_e P$ against time is approximately straight as the model predicts.

End of section exercises

Exercise 5

Write down equations resulting from the application of the 'input–output principle' to:

(i) the amount of money in your bank account;

(ii) the amount of water in a reservoir.

[*Solution on p. 46*]

Exercise 6

Table 2 gives data on the human population of the world from 1930 to 1970. Comment on the relation of the exponential growth model to this data.

[*Solution on p. 46*]

Table 2. Data on the human population of the world, estimated in millions.

Year	Population
1930	2070
1940	2295
1950	2485
1960	2982
1970	3635

2 The logistic model

2.1 Specify the real problem

I started Section 1 with a very broad task—to describe the variation of unexploited populations with time. In the light of the variety of population behaviour shown in Figure 2 of Section 1 it is hardly surprising that the model I obtained, the exponential model, is only applicable to certain populations and even then it is only reliable over restricted time domains. In this section I shall take a less ambitious trip around the 'seven box diagram'. I shall confine my attention to *increasing* populations (for example, the squirrel population in Figure 2 of Section 1) in the hope that for such populations the resulting model will be more generally applicable.

The exponential model is fairly accurate for many populations in a state of rapid increase, but it requires a restricted domain of validity to be reasonable. As a model of the behaviour of increasing populations over longer periods of time the exponential model is clearly unsatisfactory since it predicts unbounded growth. My purpose in this section will be to seek a model which gives a more realistic description of population growth.

I have a specific motive in concentrating on the case of population increase. You will recall that my underlying aim is to construct a model to help in the question of population exploitation. Unless the population would increase when unexploited, it seems certain that exploitation will cause the population to decrease, which is the situation that one hopes to avoid.

2.2 Constructing a model

In Section 1 we were concerned with the exponential model, which, in differential equation form, is

$$\frac{dP}{dt} = (B - C)P. \qquad (1)$$

Here B and C are the birth and death rates as a proportion of the population (such rates are often quoted as percentages of the total population). To emphasize this fact I shall refer to B as the **proportionate birth rate,** to C as the **proportionate death rate**, and to $B - C$ as the **proportionate growth rate** of the population.

In the exponential model B and C are assumed constant; but, if the population is to grow at all, this has the unreasonable implication of unbounded population growth. In reality some factor must limit the size of any population. The most obvious factor likely to do this is available food supply, although other factors, such as the activity of predators, may play the key role in limiting population numbers in certain circumstances.

However I am not concerned here with the mechanisms by which population levels are actually limited, only the fact that such mechanisms exist. I will now translate this idea into a specific modelling assumption. I will assume that for any particular population there is a population level at which the population is in equilibrium with its environment. When the population is at this equilibrium level, it will neither grow nor decline.

Assumption: there exists an equilibrium population level

This assumption is readily turned into a specific mathematical statement. If P denotes the population at time t, and M denotes the equilibrium population level, I am assuming that when $P = M$, $\dfrac{dP}{dt} = 0$.

How does this new assumption relate to Equation (1)? If we rewrite (1) as

$$\frac{1}{P}\frac{dP}{dt} = B - C,$$

we see that when $P = M$, the left-hand side of this equation is now required to be zero. Clearly, the assumption that $B - C$ is constant can no longer be tenable (unless $B - C$ is always zero, in which case the population is constant at its equilibrium level).

Question

How would you expect the proportionate growth rate $B - C$ to vary as P varies? Can you sketch the form a graph of $B - C$ against P might be expected to take?

Answer

I would expect that as the population increases then (i) the proportionate birth rate B might decrease (particularly for territorial species, where a decreasing *proportion* of the population would breed), and certainly would not increase, and (ii) the proportionate death rate C might increase, as individuals find food increasingly hard to find, and certainly will not decrease. Hence as P increases $B - C$ should decrease, and when P reaches M, B and C will have become equal (see Figure 1).

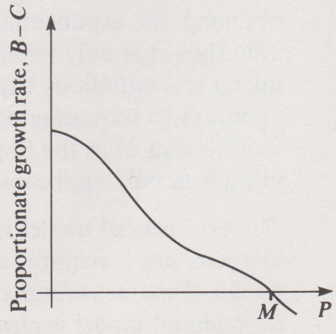


Figure 1. As the population P increases, the proportionate growth rate $B - C$ may be expected to decrease.

Formulate the mathematical problem

Let me suppose for the moment that the function for the proportional growth rate whose graph is given in Figure 1 is $g(P)$. Then we have

$$\frac{1}{P}\frac{dP}{dt} = g(P). \qquad (2)$$

If we had a specific expression for the function $g(P)$, then the mathematical problem would be to solve a differential equation—one of a form that you have met in *Unit 2*. Can we find a specific expression for $g(P)$?

The general ideas about population growth discussed above lead only to some constraints on the possible shape of the graph of $g(P)$, not to a specific equation. To obtain a specific equation I must make a further assumption. At this stage I have no theoretical ideas suggesting a particular form for $g(P)$, so I shall make a provisional assumption, based on the 'principle of simplicity'. That is, I shall, for now, assume $g(P)$ to have the simplest form consistent with my ideas so far, and pursue the consequences of this provisional assumption.

Be as simple as possible.

The simplest form $g(P)$ could take is a decreasing *linear* function of P, and I shall assume (provisionally) that it has this form. We require that $g(M) = 0$, so if g is linear it must be of the form

Assumption: g is linear

$$g(P) = a\left(1 - \frac{P}{M}\right)$$

where a is a *positive* constant (positive because we want $g(P)$ to be a *decreasing* function of P). On this assumption, Equation (1) becomes

$$\frac{1}{P}\frac{dP}{dt} = a\left(1 - \frac{P}{M}\right)$$

or

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) \qquad (3)$$

This differential equation is used very frequently in modelling population growth (and in other contexts) and has a special name—the **logistic equation**.

2.3 The implications of the model

Solve the mathematical problem

The next step is to solve the logistic equation. There are two constant solutions; $P = M$, and $P = 0$. These satisfy the equation by making both sides equal to zero. The other solutions can be found using separation of variables; there are three cases to consider, $P < 0$, $0 < P < M$, and $M < P$.

Exercise 1

(i) Find the general solution of the logistic equation subject to the condition $0 < P < M$.

(ii) Find the particular solution of the logistic equation corresponding to the initial condition $P = P_0$ when $t = 0$, and show that it can be written in the form of Equation (4) below.

[*Solution on p. 46*]

A similar method can be applied to the cases $P < 0$ and $M < P$ to give the same solution as Equation (4) with P_0 no longer restricted to $0 < P_0 < M$.

Interpret the solution

We have seen that the logistic equation has the solution

$$P = \frac{M}{1 + \left(\dfrac{M}{P_0} - 1\right)e^{-at}} \qquad (4)$$

where $P = P_0$ when $t = 0$ (and $P_0 \neq 0$).

We now examine the general features of this solution. This is not so straightforward here as in the previous section, because Equation (4) is moderately complicated.

Since our main concern is with *increasing* populations we need only consider those solutions which approach the equilibrium level M from below, that is, those for which the initial population satisfies $0 < P_0 < M$.

Exercise 2

Sketch the graph of Equation (4) for the case $0 < P_0 < M$. The specific questions below will help you to do this.

(i) How does P behave for t large and positive?

(ii) How does P behave for t large and negative?

(iii) Check that $0 < P < M$ for all values of t.

(iv) Use Equation (3) to show that P is an increasing function of t.

(v) Show that changing the value of P_0 (to P_0' say) simply shifts the curve relative to the P-axis.

[*Solution on p. 46*]

The solution to Exercise 2 shows that for $0 < P_0 < M$ the graph of Equation (4) has the general shape shown in Figure 2(a). The overall shape of the curve is independent of the particular value of P_0; solutions for different values of P_0 are obtained by moving the graph to the left or right relative to the P axis. If P_0 is small compared with M we have the situation shown in Figure 2(b), whereas if P_0 is close to M, we have that shown in Figure 2(c). The graph in Figure 2(a) is often referred to as the **logistic curve**.

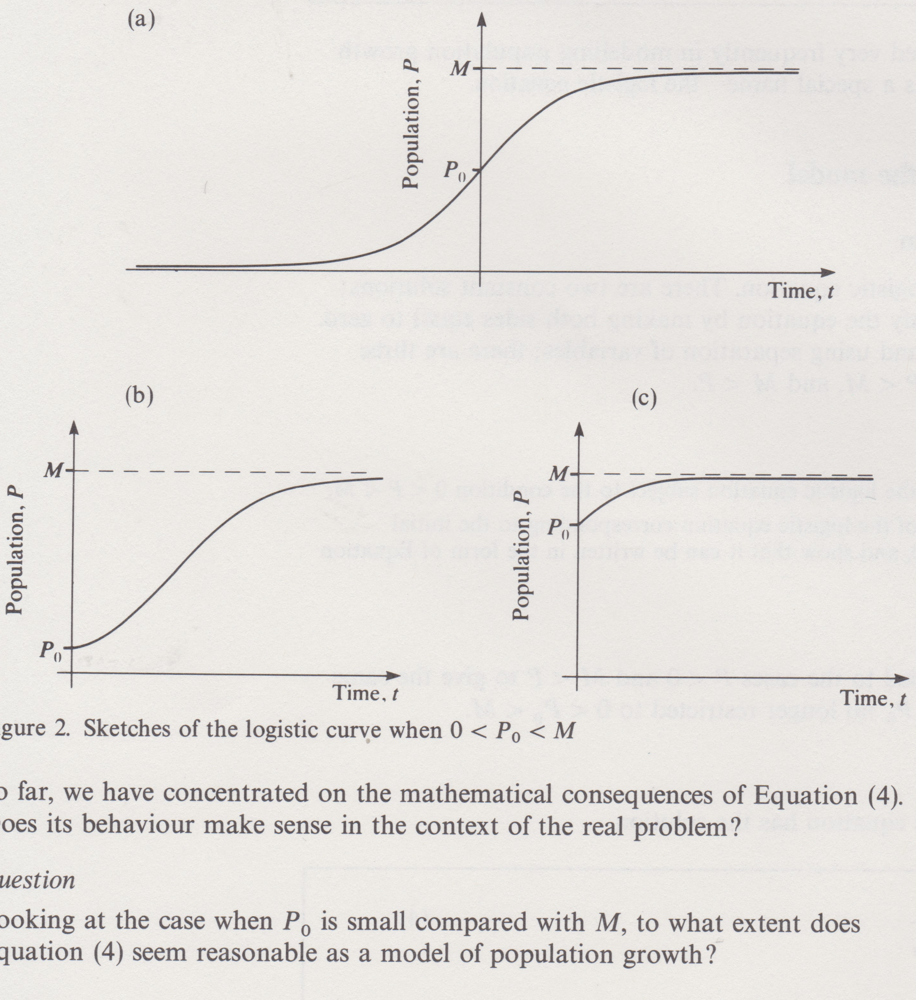


Figure 2. Sketches of the logistic curve when $0 < P_0 < M$

So far, we have concentrated on the mathematical consequences of Equation (4). Does its behaviour make sense in the context of the real problem?

Question

Looking at the case when P_0 is small compared with M, to what extent does Equation (4) seem reasonable as a model of population growth?

Answer

Looking at the situation when P_0 is small compared with M (as shown in Figure 2(b)) means that we are looking at the implications of the model for the situation where the population is initially well below its equilibrium level. The graph shows the population growing, at first at an ever increasing rate. However, as the population increases towards the equilibrium level, its growth becomes slower and

slower, and eventually the population becomes effectively constant at the equilibrium level. (I have ignored the 'fine detail' of the mathematics which implies convergence to the limiting value M as t becomes large, with this limiting value never actually being achieved. This sort of mathematical detail is not going to correspond to anything significant in reality for a model such as this.) These general features of the solution curve are those that I was looking for when constructing the model, and do seem generally reasonable. Figures 2(i) and 2(j) of Section 1 show two examples of population growth whose general shape is similar to that of Figure 2(b) here, and this is certainly encouraging. Figure 3 here shows another example.

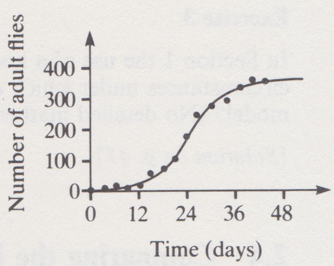


Figure 3. The growth of a laboratory population of fruit flies (*Drosophilia*) showing a generally 'logistic' shape.

With examples of data showing the same general shape as the model, the natural next step is to look at the detailed fit of data to the model. Before doing this though, I want to look at a couple of other points. The first is how, if at all, does this model relate to the exponential model of population growth? Secondly, what does the parameter a in the model *mean*? (By 'parameter' I mean an unspecified constant appearing in an expression.) We know that P_0 represents the initial population (at whatever point in time we set the model going), and M represents the postulated equilibrium population level; but what of a? (This is a general modelling point: in order to gain insight into a model, you should always seek to interpret its parameters in terms of the real problem.)

Interpret the model's parameters

It turns out that the way to answer these questions is to look at the behaviour of Equation (4) in the case when P_0 is small, for small values of t. I shall do this now.

We will approximate Equation (4) on the assumption that P_0 is small compared with M. First rearrange Equation (4) by multiplying numerator and denominator by e^{at},

$$P = \frac{M}{1 + \left(\dfrac{M}{P_0} - 1\right)e^{-at}} \tag{4}$$

$$= \frac{Me^{at}}{\dfrac{M}{P_0} + e^{at} - 1}.$$

In the denominator, $\dfrac{M}{P_0}$ is large, whereas for small values of t $\left(\text{say } t < \dfrac{1}{a}\right)$, $e^{at} - 1$ is fairly small. It follows that, for small values of t, the denominator is approximately $\dfrac{M}{P_0}$ giving

Approximate Equation (4) assuming:

1. P_0 is small compared with M,
2. $t < \dfrac{1}{a}$.

$$P \simeq \frac{Me^{at}}{M/P_0} = P_0 e^{at}. \tag{5}$$

This result corresponds with the conclusions of our previous trip around the modelling cycle. It shows that, 'under certain circumstances' (when the initial population is well below equilibrium) and 'for a limited period of time' $\left(\text{for } t < \dfrac{1}{a}\right)$, the logistic equation implies exponential growth. So the logistic model encompasses as a special case the situation where the exponential model was reasonable. It also eliminates the grossly unreasonable feature of that model—unlimited population growth—and implies a form of growth corresponding in a general way to real examples (such as Figures 2(i) and 2(j) of Section 1). So far, so good.

Relation to the exponential model

We can also use Equation (5) to place an interpretation on the parameter a. It is the proportionate growth rate that the population is able to achieve at low population levels: the difference between the proportionate birth and death rates before the biological factors limiting growth at higher population levels have a significant effect. Reference back to the construction of the model confirms this interpretation, for the proportionate growth rate is given by $g(P) = a(1 - P/M)$ which is approximately equal to a when P is small.

Exercise 3

In Section 1 the use of a linear model of population increase was considered. Are there any circumstances under which a linear model would produce the same results as the logistic model? (No detailed mathematical argument is expected, just a general comment.)

[*Solution on p. 47*]

2.4 Comparing the logistic curve with data

Table 1 gives data on the growth of three populations. In this subsection I shall examine ways of comparing such data with the logistic model. Unfortunately there is no one simple and wholly satisfactory way of doing this. I will describe briefly two ways of plotting data which are suitable for making comparisons with the logistic equation, but I will avoid a detailed examination of the technical pros and cons of various methods.

Table 1(a). The growth of a yeast population (Carlson, 1913).

hours	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
population	9.6	18.3	29.0	47.2	71.1	119	175	257	351	441	513	560	595	629	641	651	656	660	662

Table 1(b). The growth of a population of the protozoan *Paramecium aurelia* (Gause, 1934)

days	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
population	14	34	56	94	189	266	330	416	507	580	610	513	593	557	560	522	565	517

Table 1(c). The British population of collared doves (Hudson, 1965)

year	1959	1960	1961	1962	1963	1964
population	205	675	1900	4650	10200	18 855

Given data such as that in Table 1, your first instinct may well be to plot P against t, as shown in Figure 4. That is fair enough, but it can do no more than give a general picture of the data. It is of no help in obtaining a detailed fit. To do this, a helpful strategy is to look for variables that should be linearly related.

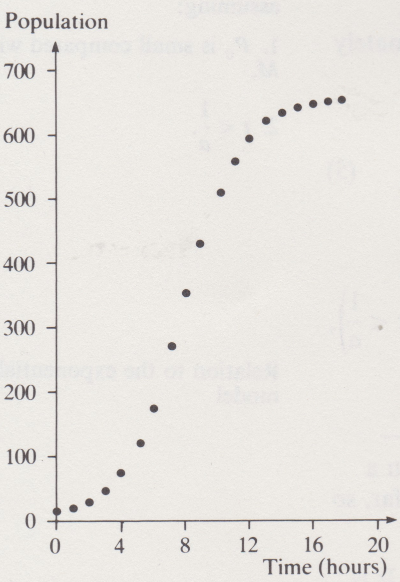


Figure 4(a). Graph of the yeast population data in Table 1(a)

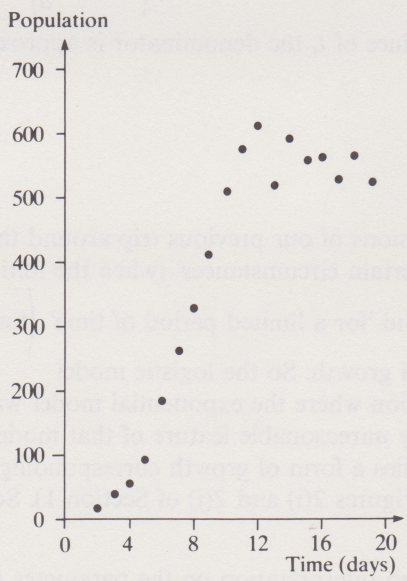


Figure 4(b). Graph of the protozoan population data in Table 1(b)

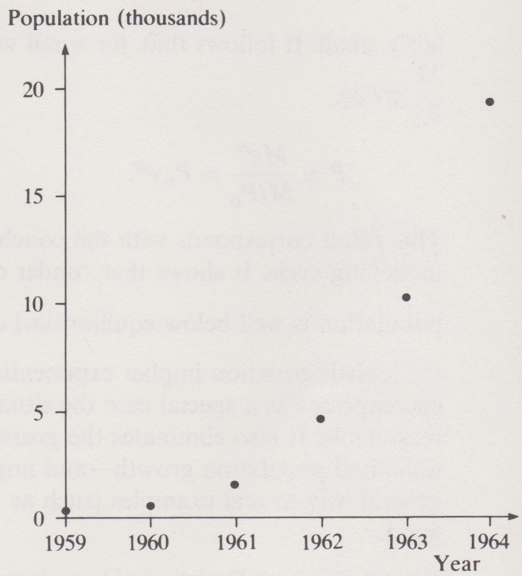


Figure 4(c). Graph of the collared dove population data in Table 1(c)

Question

Start to rearrange Equation (4) as if you were making t the subject, and hence find two variables which are linearly related.

Is there a graph that should be straight?

Answer

Equation (4) can be rearranged as follows

$$P = \frac{M}{1 + \left(\frac{M}{P_0} - 1\right)e^{-at}} \quad (4) \qquad \text{so} \qquad 1 + \left(\frac{M}{P_0} - 1\right)e^{-at} = \frac{M}{P}$$

$$\text{i.e.} \qquad \left(\frac{M}{P_0} - 1\right)e^{-at} = \frac{M}{P} - 1 \quad (6) \qquad \text{hence} \quad \log_e\left(\frac{M}{P_0} - 1\right) - at = \log_e\left(\frac{M}{P} - 1\right).$$

Thus the logistic equation implies that the variables $\log_e\left(\frac{M}{P} - 1\right)$ and t are linearly related. This suggests that we plot $\log_e\left(\frac{M}{P} - 1\right)$ against t and look for linearity. There is one difficulty here, though. The variable we wish to plot contains M, which is an unknown parameter. So to use this procedure one must first estimate the size of the equilibrium population M.

Question

(i) Estimate a value for M for the data in each of Tables 1(a) and 1(b).

(ii) Use the method described above to test the data in Table 1(a) to see if it fits the logistic model.

(iii) Can you see any difficulties in using this method to test the data in Table 1(b)? How about the data in Table 1(c)?

Answer

Looking at Figure 4(a), we can see that the data in Table 1(a) increases throughout and has nearly become constant. It seems reasonable to estimate M as just above the later values—say $M = 665$. The data in Table 1(b) do not behave quite so nicely, reaching a maximum (at 610) then oscillating up and down to a certain extent. The level at which the population would be in equilibrium seems to be somewhere between 610 and 510. A reasonable estimate would seem to be about 550. (There are more systematic ways of arriving at an estimate for M, but this procedure is adequate for my purposes here.)

Figure 5 shows the results of plotting $\log_e\left(\frac{M}{P} - 1\right)$ against t for the data in Table 1(a) with $M = 665$. The fit obtained is certainly satisfactory.

hours	amount of yeast, P	$\frac{M}{P} - 1$	$\log_e\left(\frac{M}{P} - 1\right)$
0	9.6	68.27	4.223
1	18.3	35.34	3.565
2	29.0	21.93	3.088
3	47.2	13.09	2.572
4	71.1	8.353	2.123
5	119	4.588	1.523
6	175	2.800	1.050
7	257	1.588	0.462
8	351	0.895	−0.111
9	441	0.5079	−0.677
10	513	0.296	−1.216
11	560	0.187	−1.674
12	595	0.1176	−2.140
13	629	0.0572	−2.861
14	641	0.0374	−3.285
15	651	0.0215	−3.839
16	656	0.0137	−4.289
17	660	0.0076	−4.883
18	662	0.0045	−5.397

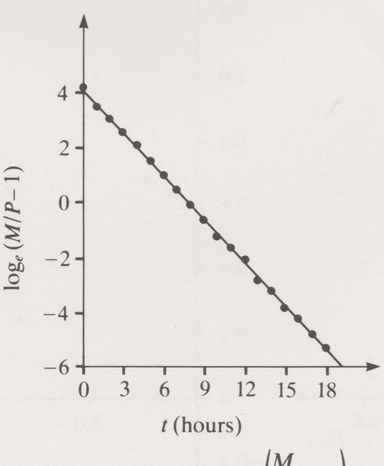


Figure 5. A plot of $\log_e\left(\frac{M}{P} - 1\right)$ against t, with $M = 665$, for the population data in Table 1(a).

There is a difficulty in attempting to use this method of fitting for the data in Table 1(b). Any reasonable estimate of M in that case will be smaller than some of the observed values of P. For these values of P, $\dfrac{M}{P} - 1$ is negative, so $\log_e\left(\dfrac{M}{P} - 1\right)$ cannot be plotted. For the data in Table 1(c) plotted in Figure 4(c) a value for M cannot be estimated by eye, and so the method cannot be used.

Thus, although we have managed one favourable comparison of data with the logistic, the method sometimes leads to difficulties. With ingenuity however, alternative ways of comparing the logistic model with data can be found. The next exercise describes one approach. Again, we look for two variables that the logistic implies are linearly related.

Exercise 4

We consider the situation in which population data are available at *equal* time intervals. (In a sense this is a simplification of the problem since data will not always be so convenient.) Denote by P_n the population after n intervals of time. We assume that P_n is given by the logistic equation, so that

$$P_n = \frac{M}{1 + Ke^{-an}}$$

(where $K = \dfrac{M}{P_0} - 1$ is a constant).

(i) Use Equation (6) to obtain expressions for $\dfrac{M}{P_n} - 1$ and $\dfrac{M}{P_{n+1}} - 1$. Eliminate n from the equations you obtain, to show that

$$\frac{M}{P_n} - 1 = e^a\left(\frac{M}{P_{n+1}} - 1\right)$$

(ii) Multiply both sides of the above result by P_{n+1} and hence show that the variables $\dfrac{P_{n+1} - P_n}{P_n}$ and P_{n+1} are linearly related. (Other pairs of variables are also linearly related. I will explain why I have made this particular choice in Subsection 2.5.)

(iii) If a population satisfies the logistic equation, a plot of $(P_{n+1} - P_n)/P_n$ against P_{n+1} will give a straight line. Show that this line intersects the P_{n+1} axis at M and the $(P_{n+1} - P_n)/P_n$ axis at $e^a - 1$.

(iv) Figure 6 shows plots of $\dfrac{P_{n+1} - P_n}{P_n}$ against P_{n+1} for the data in Table 1. Comment on these plots.

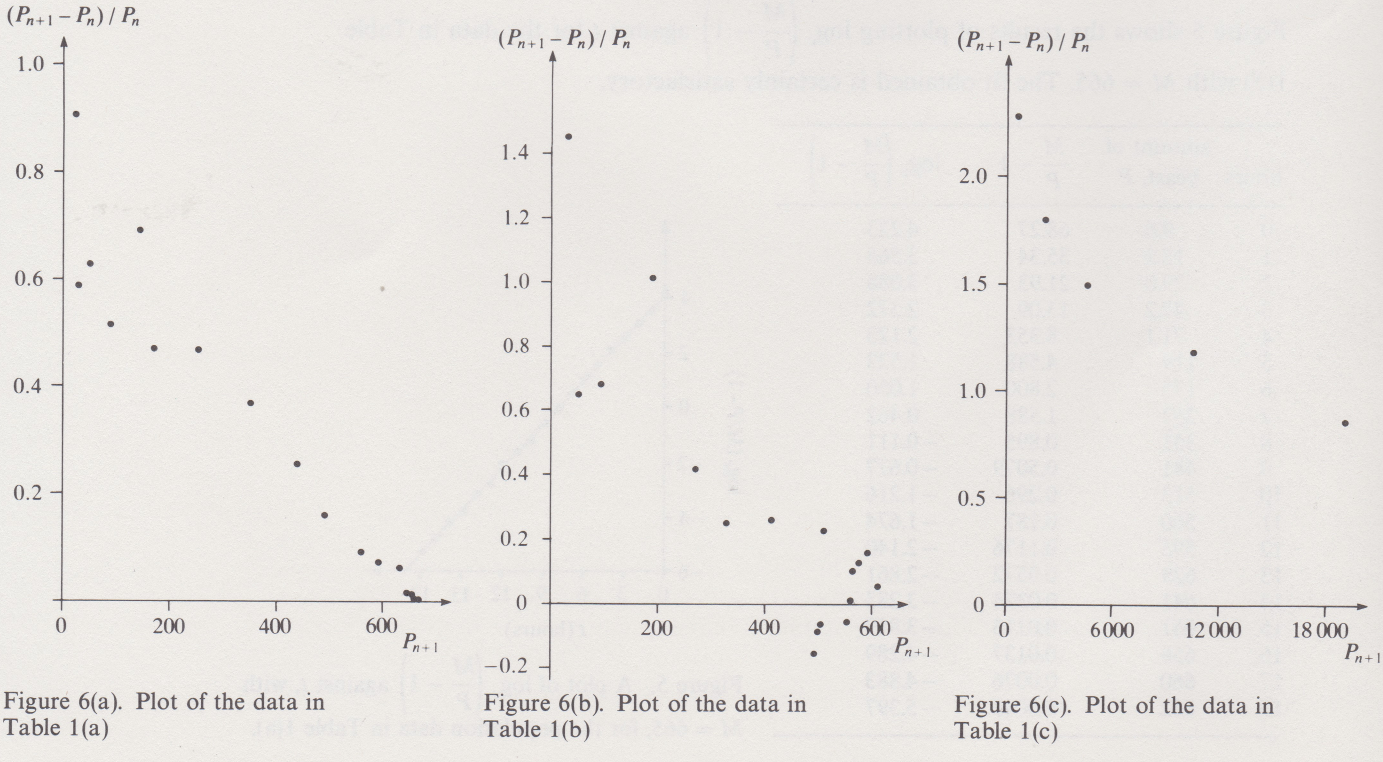


Figure 6(a). Plot of the data in Table 1(a)

Figure 6(b). Plot of the data in Table 1(b)

Figure 6(c). Plot of the data in Table 1(c)

(v) The straight line of least squares best fit to the data in Figure 6(b) has equation

$$\frac{P_{n+1} - P_n}{P_n} = 1.0396 - 0.0018433P_{n+1}.$$

Using the result in (iii) estimate the parameters M and a. Comment on the likely accuracy of these estimates.

[*Solution on p. 47*]

Exercise 4 shows that the logistic curve is a reasonable fit to data if the graph of $(P_{n+1} - P_n)/P_n$ against P_{n+1} can be fitted by a straight line. If it can, the intersections of the line with the axes can be used to estimate the parameters M and a, for the line intersects the P_{n+1} axis at M and the $(P_{n+1} - P_n)/P_n$ axis at $e^a - 1$.

The logistic curve for the data in Table 1(b) with the values of M and a calculated in Exercise 4 is shown in Figure 7.

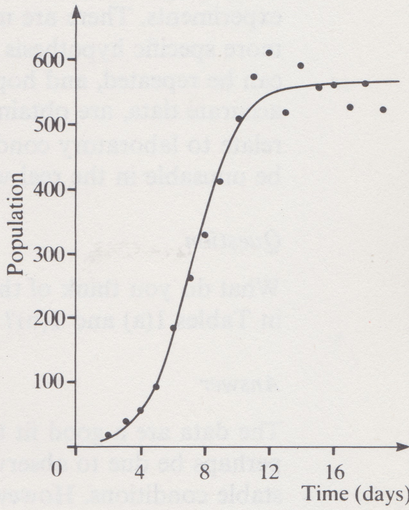


Figure 7. A comparison of the data plotted in Figure 2(b) with a logistic curve plotted using the parameter values $M = 564$, $a = 0.713$ calculated in Exercise 4(v).

The method of fitting data to the logistic described in Exercise 4 does not require a prior estimate of M and may be used for any data. However, it tends to exaggerate small inaccuracies in the data and so gives the impression that the fit of the logistic model to data is worse than in fact it is.

2.5 'Evaluating' the logistic model

We have now seen examples of data that fit the logistic equation quite well (and other examples could be given). Of the examples in Figure 2 of Section 1, two—(i) and (j)—show the general shape of the logistic curve, and others—(b), (c), (k) and (l)—the shape of part of the logistic curve. However the patterns of population change shown by the examples in (a), (f), (g), (h) and (m) are not consistent with the implications of the logistic model. This is perhaps disappointing, but it should be no great surprise.

A number of assumptions were made in setting up the logistic model, and these are presumably not universally applicable. To see why the logistic model is unsuitable in some cases we will look back to the assumptions built into the model.

Question

What are the major assumptions made in setting up the logistic equation?

Answer

Three important assumptions are listed in the box below. The first two were made explicitly, the third is implicit in the model.

Assumptions of the logistic equation

1. That an 'equilibrium population' M exists, which is independent of time.
2. That the right-hand side of Equation (3) has a *linear* form.
3. That birth and death rates respond *instantly* to changes in population level.

Let us look at these in turn.

It seems reasonable enough to suppose that in any given situation there is a population level that would be in equilibrium with its environment. (When there is just enough food, and no more, perhaps.) The problematic feature of (1) is the assumption that M is constant. The habitat of animal populations in the wild is subject to variation, and so the 'equilibrium population' M will vary with time. This fact means that a hypothesis of the form 'increasing populations will grow according to Equation (3)', is bound to be incorrect—it is too ambitious. A

feasible hypothesis is 'in a perfectly stable environment, a population will grow according to the logistic equation'. Perfectly stable environments do not occur in practice, of course, but it is common scientific practice to formulate laws that only work under 'ideal' conditions. But this remains only a *hypothesis* of course, it is not proved. How might this hypothesis be tested?

The best approximation to a 'perfectly stable environment' can be provided in a laboratory. The data in Tables 1(a) and 1(b) do in fact relate to laboratory experiments. There are many advantages to experimental data: they allow this more specific hypothesis to be tested; they are reproducible—the same conditions can be repeated, and hopefully lead to similar results; more readings, and more accurate data, are obtained. They do have one disadvantage in that they do only relate to laboratory conditions, and hypotheses supported in the laboratory may be unusable in the real world. (The 'ideal' may depart too far from the 'real'.)

Role of experiments

Question

What do you think of the above hypothesis, in the light of the experimental data in Tables 1(a) and 1(b)?

Answer

The data are a good fit to the logistic equation. The fit is not perfect; this could perhaps be due to observational inaccuracy, or an inability to maintain perfectly stable conditions. However there is one particular feature of note. That is the tendency of the later observations in Table 1(b) to a small but steady oscillation. Whatever the values of the parameters a, M and P_0, the logistic curve (Figure 2) never shows such oscillations. This suggests that, although the logistic model may be a good fit here, it is not the full story. The hypothesis above is not a 'law', even under 'ideal' conditions. This is hardly surprising in the light of Assumption (2) noted above; the choice of a linear function for the proportionate growth rate was purely on the grounds of simplicity—many other functions have the general properties suggested by the arguments proposed earlier in the section.

Recalling Assumption (2) suggests another form of verification that would be useful. Is there any way we can examine Assumption (2) *directly*?

Question

Can you suggest a way of using the data in Table 1 to check directly whether the proportionate growth rate $g(P)$ in the equation

$$\frac{1}{P}\frac{dP}{dt} = g(P)$$

is a linear function of P?

Answer

One way would be to use the data to plot $\dfrac{1}{P}\dfrac{dP}{dt}$ against P. This would give a graph of $g(P)$ which we could test for linearity. Although no data is given for the derivative $\dfrac{dP}{dt}$, it is approximately equal to the increase of population over unit time intervals, that is $P_{n+1} - P_n$. It is not clear whether we should choose P_n or P_{n+1} for P, but making one possible choice, we could plot $\dfrac{P_{n+1} - P_n}{P_n}$ against P_{n+1}. In fact, this has already been done in Exercise 4, but now, the graphs in Figure 6 can be regarded as approximate graphs of $g(P)$ and the linearity of these graphs can be regarded as direct tests of Assumption (2).

A more sophisticated approach to verifying Assumption (2) is to construct a laboratory experiment in which the proportionate growth rate, $g(P)$, of a population is observed directly, at various population levels. This can be done, and the results of one such experiment are shown in Figure 8.

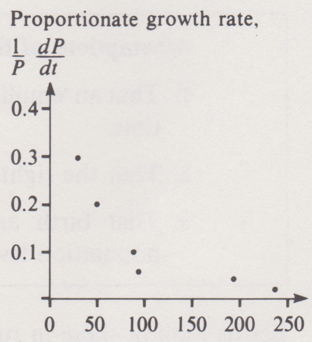


Figure 8. The results of an experiment in which a population was maintained at various constant densities and the corresponding proportionate growth rates observed. (The results shown are averages of those obtained by Smith, 1963.)

Question

Comment on Assumption (2) in the light of Figure 6(c) and Figure 8.

Answer

The examples in Figures 6(c) and 8 show that the linear form of the right-hand side of Equation (3) is not always supported in practice. They suggest that in some cases a more accurate model of population growth may be obtained by a different choice of $g(P)$ in

$$\frac{1}{P}\frac{dP}{dt} = g(P). \qquad (2)$$

However, although we may be able to find a more suitable form for $g(P)$ in particular examples, we have no grounds for preferring some other form in *general*. In fact the growth curves implied by other choices of $g(P)$ are often similar in general shape to the logistic curve (Figure 2).

The logistic equation provides a surprisingly accurate fit to some population data, but more often it provides a good general picture of population growth, whose details may not be accurate. The moral is to use the logistic equation realistically, in an awareness of its limitations.

Exercise 5

The logistic equation implies that the equilibrium levels M for the populations in Tables 1(b) and 1(c) may be estimated by fitting straight lines, as shown in Figure 9, and seeing where they intersect the P axis. What reliance would you place on this procedure in each case?

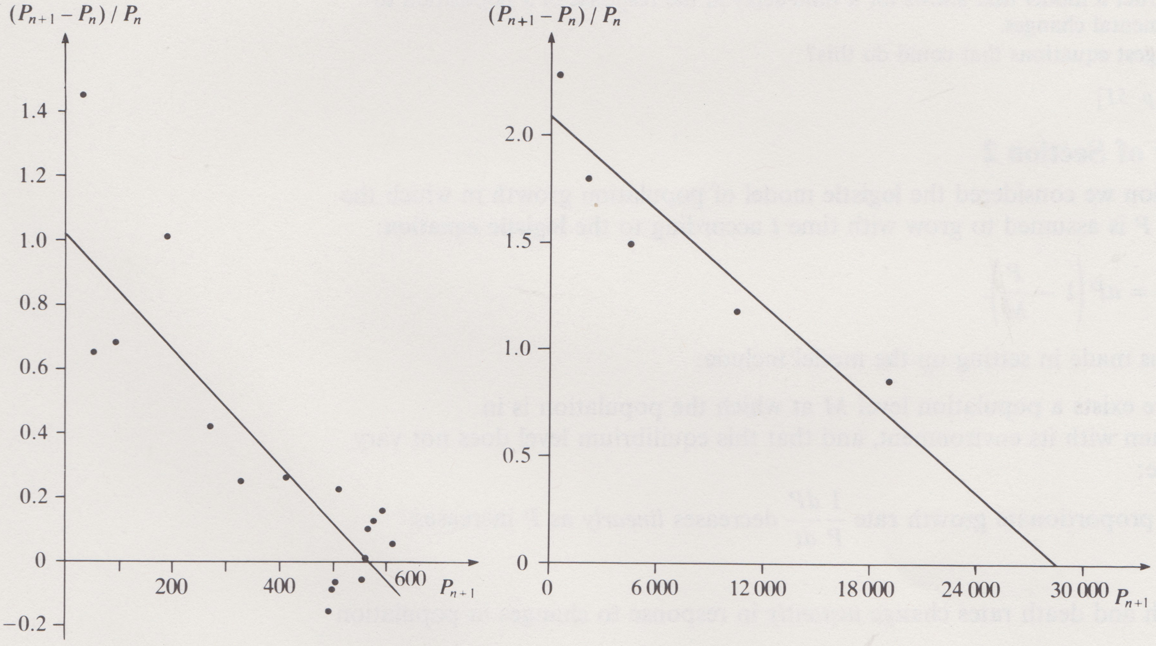


Figure 9(a) The plots in Figure 6(b) with a straight line drawn to estimate the equilibrium population.

Figure 9(b) The plots in Figure 6(c) with a straight line drawn to estimate the equilibrium population.

[*Solution on p. 47*]

It is possible in some circumstances to work with a general model of the form of Equation (2) without assuming a specifically linear form for the right-hand side. This approach is preferable, where it is possible, for the implications of such a general model are more robust than those of the logistic model. This approach is adopted to some extent in the model of exploitation discussed in Section 4.

Assumption (3) mentioned above brings out a factor that may be the underlying cause of oscillations in the level of some populations. For example, a population may increase above the level that the environment can *consistently* support, but

this may have no effect on births and deaths until several years later, when there has been a considerable reduction in available food through, say, overgrazing and the death rate increases due to starvation. The population will then fall below the possible long-term equilibrium, for its food resources will have been depleted. Eventually, when the population falls to a low enough level, its food resources begin to increase. Later the population increases again, and so the cycle repeats itself.

Iterate?

Should we attempt to improve the logistic model of the growth of an unexploited population? The answer to this question depends on one's purpose. My *original* purpose was to investigate the effect of exploitation on a population. I will next look at a model, based on the logistic, that takes exploitation into account. My criterion for judging the logistic (for my original purpose) should be its success or failure in the context of this model of exploitation.

Were we simply looking for as good a model as possible of the growth of an unexploited population, there are a number of lines of investigation one could pursue. Consideration of these may help you to review my discussion of the logistic model in this section.

Problem 1

This question requires originality—it is not a routine test of your understanding of the section. One strategy for answering it would be to jot down ideas as they occur to you, and return to the question when you have completed your study of the unit.

By considering the strengths and weaknesses of the logistic model, try to suggest possible lines of further investigation. For example, you might wish

(i) to look for a model that takes the variation of the environment with time into account

(ii) to construct a model that allows for a time-delay in the response of a population to environmental changes.

Can you suggest equations that could do this?

[*Solution on p. 51*]

Summary of Section 2

In this section we considered the **logistic** model of population growth in which the population P is assumed to grow with time t according to the **logistic equation**:

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right).$$

Assumptions made in setting up the model include:

1. that there exists a population level M at which the population is in equilibrium with its environment, and that this equilibrium level does not vary with time;
2. that the proportionate growth rate $\dfrac{1}{P}\dfrac{dP}{dt}$ decreases *linearly* as P increases, and
3. that birth and death rates change *instantly* in response to changes in population size.

The solution of the logistic equation is

$$P = \frac{M}{1 + \left(\dfrac{M}{P_0} - 1\right)e^{-at}}$$

where $P = P_0$ when $t = 0$. The graph of this equation (see Figure 10) is called the **logistic curve**.

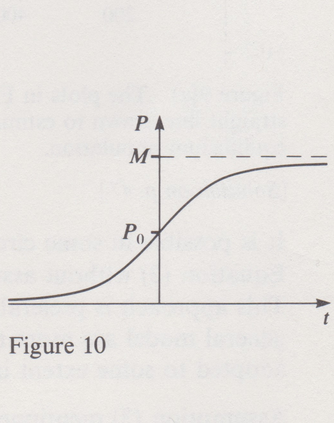


Figure 10

The parameter M is the equilibrium population whose existence is presumed in Assumption (1) above.

If P_0 is small compared with M, and $t < 1/a$ say, then the solution of the logistic equation is approximately of the exponential form $P = P_0e^{at}$. We see therefore that

a represents the proportionate growth rate of which the population is capable, at low population levels.

Two ways of comparing the logistic curve with data were considered:

1. First estimate M, then plot $\log_e\left(\frac{M}{P} - 1\right)$ against t.

2. If data is available at equal intervals of time, and P_n is the nth data value for P, plot $\frac{P_{n+1} - P_n}{P_n}$ against P_{n+1}.

The implications of the logistic model were considered in the light of a number of examples of population data. We saw examples where the population growth with time implied by the logistic equation corresponded well with real data, but we also saw examples where attempts to verify Assumption (2) directly failed. We have also seen some examples of populations that have undergone periods of growth that correspond very little with the logistic curve. These include populations that undergo very large, but apparently random, variations in size (for example, the moth population in Figure 2(f) of Section 1), and populations that undergo systematic oscillations in level (for example, the lynx in Figure 2(g) of Section 1).

For some populations Assumptions (1) and (3) above are too far from reality for the logistic model to be of any value.

Many of the examples supporting the logistic model relate to laboratory experiments, in which Assumption (1) is more likely to hold; but some relate to wild populations, suggesting that the model can be of value outside the laboratory. If a population is at a level well below that which the environment can consistently support, then the logistic equation will often provide a qualitative description of the way it will grow back towards its equilibrium level. It cannot be relied on to provide an *accurate* description of the actual growth of a wild population, because of the random factors (such as hard winters) that may affect a population at a particular time, and because the specific form of the right-hand side of the logistic equation will not always be the most appropriate for a particular example. For example, the logistic model implies that in the long term a population will become *precisely* constant, but this is not what is observed in practice.

For a wild population, the qualitative implications of the logistic equation may well be appropriate, but accuracy should not be expected.

End of section exercises

Exercise 6

Suggest two ways in which Assumption (2) on page 25 can be examined directly.

[*Solution on p. 48*]

Exercise 7

Figure 11 shows a plot of $\log_e P$ against t for hypothetical population data. Use it to estimate the parameters a and M for a logistic curve to fit this data.

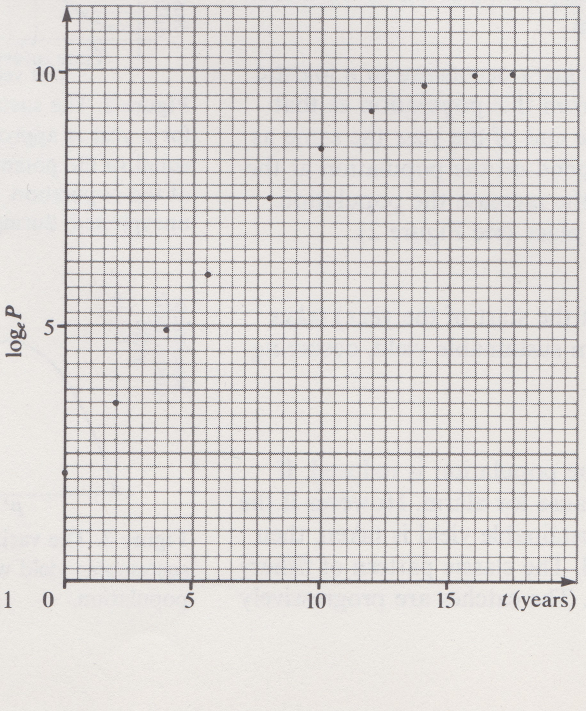


Figure 11

Is this a useful method of comparing the logistic model with data for validation purposes?

[*Solution on p. 48*]

Exercise 8

Suggest (briefly) reasons why the populations in Figures 2(f) and 2(g) of Section 1 vary in ways that depart so far from the implications of the logistic model.

[*Solution on p. 48*]

Exercise 9

In Subsection 1.2 we saw an example of data that was fitted by an exponential, but for which *linear* extrapolation provided a better estimate of future populations than did exponential extrapolation. Briefly, suggest a possible explanation for this.

[*Solution on p. 48*]

3 Fishing (Television Section)

TV

TV3

3.1 Preliminary work

In this section we consider the use of mathematical models to estimate the appropriate levels of catch in the fishing industry. If you have read Sections 1 and 2 of the unit, there is no preprogramme reading. If you have not, you should look at the paragraph below.

The programme assumes that you have met the logistic equation, which is discussed extensively in Section 2. However it is not necessary to have read that section to follow the programme. You need only know that the logistic equation

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right)$$

is a possible model of the growth of an unexploited population P with time t. The graph of the solution of this equation (the logistic curve) is shown in Figure 1. The parameter M represents the level at which the population is in equilibrium with its environment.

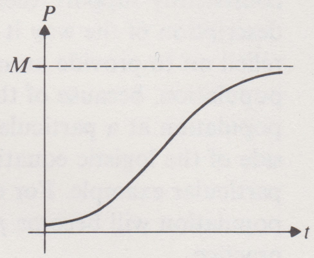


Figure 1

Now view the television programme 'Fishing for figures'.

3.2 Summary of the programme

Under certain circumstances, catches from a fishery may collapse. The programme gave a qualitative description of why this may happen.

Suppose that, if unexploited, a fish population would grow according to a logistic curve (Figure 1). Let us define the sustainable yield from this population as that annual catch which would leave the population at the end of the year the same as it was at the beginning. The sustainable yield will depend on the population at the start of the year and will be approximately equal to the increase the population would have experienced if no exploitation had taken place (see Figure 2).

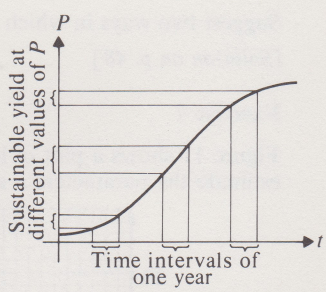


Figure 2. The sustainable yield for a year is approximately equal to the potential growth of the population, if unexploited, during the year.

A graph of sustainable yield Y against population (at the start of the year) takes the form of Figure 3. We see that there is a maximum sustainable yield, occurring at $P = P'$, say.

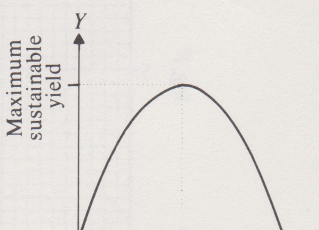


Figure 3. The variation of sustainable yield with population.

If the annual catch is above sustainable yield, then the population is reduced. If the population is well above the value P' this is no cause for alarm. However if the population is already below P', and a catch above sustainable yield is taken, then reducing the population reduces the sustainable yield. The classic pattern of fishery collapse is a series of catches above sustainable yield. The catches are progressively

smaller, but so long as they are above sustainable yield, the population, and so the sustainable yield, is also progressively reduced (see Figure 4).

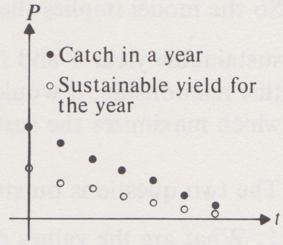


Figure 4. Pattern of fishery collapse, with catches reducing, but above the sustainable yield each year.

A procedure that may be used to estimate the maximum sustainable yield from a fishery was described. Suppose that data is available on the catches from a fishery in past years. Data may also be available on a second variable, the fishing effort exerted. It is not straightforward to put an exact figure on the amount of effort being put into catching fish in a particular fishery. However, reasonable measures can be found; for example we can multiply the tonnage of each vessel by the time spent fishing, and add the results for all the vessels exploiting the fishery during a year.

Modelling assumption

It is usual to relate the actual population to these variables by assuming that the catch per year C is proportional to the product of the population P and the fishing effort f. That is

$$C \propto Pf, \qquad \text{or} \qquad P \propto \frac{C}{f}.$$

On this assumption, catch rate per unit effort C/f may be regarded as a measure of population (remembering that there is a proportionality constant lurking in the background).

Modelling assumption

Let us assume that the population would grow according to a logistic equation, if there were no fishing. Then, taking into account fishing at a rate C, the exploited population P changes according to the equation

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - C. \tag{1}$$

Now C is proportional to fP, so

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - \lambda fP$$

where λ is a constant.

Let us assume for now that the fishing effort f exerted is also a constant. In the long-term, we would expect the population to settle at an equilibrium level. (This point is discussed in more detail in Section 4.) At equilibrium the population is constant and so $\dfrac{dP}{dt} = 0$. Hence the equilibrium population level P_E must satisfy

$$0 = aP_E\left(1 - \frac{P_E}{M}\right) - \lambda fP_E.$$

Thus,

$$P_E = 0 \qquad \text{or} \qquad 0 = a\left(1 - \frac{P_E}{M}\right) - \lambda f.$$

The solution $P_E = 0$ is of no great interest! The second solution may be rearranged as

$$P_E = M\left(1 - \frac{\lambda}{a}f\right).$$

Thus there is a positive equilibrium value for the exploited population, so long as $f < \dfrac{a}{\lambda}$. Once the population has reached this equilibrium level P_E, fish are being caught at the rate $P_E\lambda f$ without changing the size of the population. The catch rate $P_E\lambda f$ is therefore the theoretic sustainable yield corresponding to the fishing effort f. If we denote this sustainable yield by Y then $P_E = \dfrac{Y}{\lambda f}$ and we can write

$$\frac{Y}{\lambda f} = M\left(1 - \frac{\lambda}{a}f\right). \tag{2}$$

So the model implies the quadratic relationship $Y = \lambda f M\left(1 - \dfrac{\lambda}{a}f\right)$ between the sustainable yield Y and fishing effort f. If we knew values for the parameters in this relationship, it would be an easy matter to calculate the fishing effort f which maximizes the sustainable yield Y.

The two questions outstanding are:

1. What are the values of the parameters in Equation (2)?
2. Is Equation (2) reasonable, and does it correspond to real data?

To answer these questions, we need to relate Equation (2) to the real data available, that is, to the actual values of catch C and fishing effort f in various years. At this stage we run into the difficulty that Equation (2) relates to an equilibrium situation in which a *constant* fishing effort has been exerted for some time, whereas in reality the fishing effort is different each year.

To overcome this difficulty we average the fishing effort over n year intervals (the most suitable value for n depends on the fishery). We then think of the population at the end of each such interval as having resulted from n years of exploitation at this constant, average fishing effort. Thinking of the data in this way suggests that Equation (2) can be related to the real data by assuming that the population in a given year (measured by C/f) is the equilibrium population level corresponding to a constant fishing effort equal to the average fishing effort over the previous n years. Thus data on actual catch rate per unit effort C/f in a given year is plotted against the average effort taken over the previous n years. The empirical relation so obtained is then used as a model of the steady-state relationship between Y/f and f. If this relationship shows a linear trend then we can assume that Equation (2) corresponds reasonably well with reality.

Provided there is a reasonable straight line fit to this plot of C/f against average f, we can obtain an explicit linear relationship of the form

$$\frac{Y}{f} = r - sf$$

where r and s are constants. Then

$$Y = (r - sf)f.$$

It is then straightforward to calculate the maximum value of Y—the maximum sustainable yield. The value of f—the fishing effort—at which this occurs may also be found. This whole procedure is known as the **Schaefer model** (after its inventor).

Thus, in the Schaefer model we have a method of estimating the maximum sustainable yield from a fishery, and the appropriate level of fishing effort to achieve this. How useful are these estimates in practice? Questions like this do not, unfortunately, have clear-cut answers. The estimates obtained from the Schaefer model are certainly better than nothing. If no information was available other than that on catch and fishing effort, then the Schaefer model could be used as a basis for the control of a fishery. However, there are methods of obtaining better estimates of sustainable yields than those supplied by the Schaefer model.

The Schaefer model is based on two assumptions. Firstly that if it were not fished, the population would grow according to a logistic equation. Secondly that the data can be related to the model by assuming that it relates to a steady-state situation, in the way described. Surprisingly it is in the first rather than the second of these assumptions in which the key to improving our estimate of sustainable yields lies.

The logistic equation is based on the assumption that births and deaths (for the unexploited population) are related by the expression

$$\text{births} - \text{deaths} = aP\left(1 - \frac{P}{M}\right).$$

By implication this assumes that births and deaths are each well-defined functions of population size. In reality, this is not so. Figure 5 shows a plot of the number of births (the recruitment) against the population size (the spawning stock biomass) for a particular fishery.

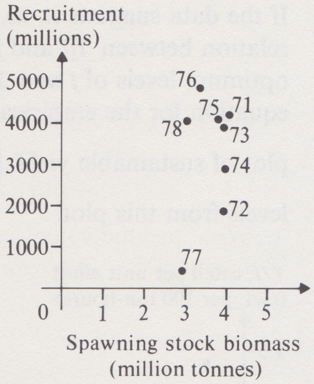


Figure 5. Data on births (recruitment) and population size (spawning stock biomass) for the western stock of mackerel between the years 1971 and 1978.

There is a connection between population size and recruitment, but there is also a great deal of variability in the annual recruitment not related to population size (which, in the present state of knowledge, is not predictable).

A great deal of the effort of the Fisheries Research Laboratory at Lowestoft is therefore devoted to discovering the actual numbers recruited each year, and the surviving strengths of various 'year-classes' (those fish born in a particular year). This is done by sampling commercial catches of fish and determining the age of the fish examined. The sampling also reveals the weight of the fish of various ages. (The weight continues to increase throughout the life of a fish.)

With this information about the population, it is then possible to calculate the weight of fish that will be caught at any particular level of fishing.

Fisheries at present are controlled through catch quotas. These are ceilings on the total weight of fish of a particular species that should be taken annually in any particular fishery. The allowable quotas are recalculated annually on the basis of the most up-to-date information on the population structure, from the sampling programme.

However the calculation of quotas by this procedure requires an estimate of the appropriate level of fishing. For this we may refer back to the Schaefer model, described earlier.

We may use that procedure to determine the most appropriate level of fishing effort in a fishery (to within an accuracy of 10 or 20%). Quotas on catch can then be calculated based on this level of fishing, and using the detailed information on various year classes from the sampling programme. Quotas calculated by this procedure take into account the state of the population at a given moment and so are more sensible than just using the estimate of maximum sustainable yield obtained from the Schaefer model.

Thus we can use the Schaefer model, based on the logistic, to calculate the appropriate level of fishing. To calculate actual quotas, we get greater accuracy if we also take into account the most important way in which that model deviates from reality. This is the extent to which annual recruitment varies, in a way not explained by variations in population size.

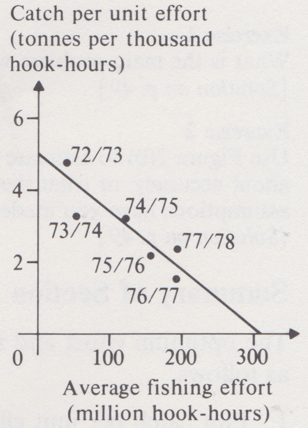


Figure 6. The catch per unit effort for the Cornish handline mackerel fishery, plotted against total international fishing effort for the western mackerel fishery.

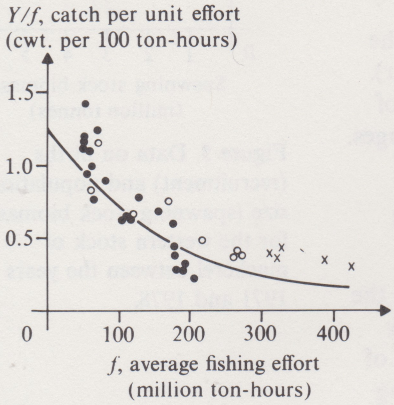
As an example the programme looked at the exploitation of the western population of mackerel (caught off South West Britain in the winter and in the Northern part of the North Sea in the summer). For that stock recent estimates of annual sustainable yields based on detailed population analysis have not in fact differed significantly from the estimate of maximum sustainable yield given by the Schaefer model. Both are about 400 000 tonnes. Recent catches however have been over 600 000 tonnes, and the total stock is estimated to have fallen from 4 million tonnes in 1974 to 2 million tonnes in 1980. This overfishing is the result of a lack of effective international enforcement of quotas.

Figure 6 shows the data on catch per unit effort plotted against effort for this fishery between the years 1972 and 1978. Note that in this example the catch per unit effort data is that for only a small part of the fishery (handline off Cornwall). However this is still a reasonable estimate of population size.

3.3 Post-programme notes and exercises

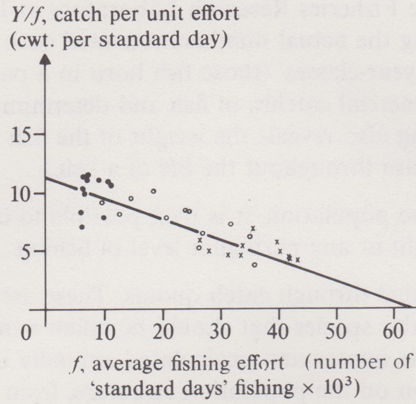
In Section 2 we saw that the specific form of the right-hand side of the logistic equation may not always be the most appropriate in particular examples. In the Schaefer model, we assumed that the unfished population would grow according to a logistic equation. If an equation with a different form of right-hand side were in fact more appropriate, we would not expect to obtain a linear relation between Y/f and f.

If the data suggests it, as, for example, in Figure 7(a), an empirical non-linear relation between Y/f and f can be fitted. If this is done, we can still estimate the optimum levels of f and Y by the same sort of procedure, but if we have no specific equation for the empirical curve we will have to use computation to obtain the plot of sustainable yield $\left(\text{equal to } \dfrac{Y}{f} \times f\right)$ against f, and then read off the optimum levels from this plot.



• data collected between 1907–38
○ data collected between 1947–53
× data collected between 1954–58

Figure 7(a). Plot of catch per unit effort against mean effort for the catch of haddock by English trawlers off Iceland.



• data collected between 1934–44
○ data collected between 1945–55
· data collected between 1956–67

Figure 7(b). Plot of catch per unit effort against mean effort for the catch of yellowfin tuna in the Eastern Tropical.

In practice, there is usually too much scatter in the data (see Figure 7(b)) to distinguish any more satisfactory relation than a linear one between Y/f and f, and so this is usually used, as it was for the mackerel fishery discussed in the programme. For fisheries, the main problem with a model based on the logistic equation is not this sort of deviation from the logistic.

Exercise 1
What is the main problem with basing fisheries models on the logistic equation?
[*Solution on p. 49*]

Exercise 2
Use Figure 7(b) to estimate the maximum sustainable yield for that fishery. (Do not worry about accuracy, or what the units are! Just make sure you know the method.) What assumptions have you made?
[*Solution on p. 49*]

Summary of Section 3

The optimum effort and maximum sustainable yield for a fishery may be estimated as follows.

1. Plot catch per unit effort for each year against the mean effort for the preceding n years.
2. Fit a straight line to the data in (1), and assume this to be the relation of sustainable yield per unit effort to sustained effort.
3. Obtain the relation between sustainable yield and sustained effort, and find its maximum. This procedure assumes
   (i) that the unexploited population grows according to the logistic equation,
   (ii) that the procedure in (2) gives a reasonable model of an equilibrium situation from historical data on actual catches, and
   (iii) that catch is proportional to the product of population and fishing effort.

This procedure is called the **Schaefer model**. It only gives the maximum sustainable yield that can be taken on average. The appropriate quota in any particular year must also take into account the actual year-class strengths, which show considerable variations not determined by population size.

End of section exercises

Exercise 3
(i) When is it sensible to take more than the sustainable yield in a given year?
(ii) When is it sensible to take less than the sustainable yield in a given year?

[*Solution on p. 49*]

Exercise 4
It is quite possible that the conditions underlying the Icelandic haddock fishery, for which data are given in Figure 7(a), have changed since 1907. Is there anything in the data to suggest that this is the case? If it were, how best might the optimum level of fishing effort be estimated from the data?

[*Solution on p. 49*]

4 Modelling exploitation

We saw in Section 2 that the logistic equation is often a reasonable model of the growth of a population when unexploited. We can now move on to model the effect of *exploitation* on a population.

Let us assume that if the population were unexploited it would grow according to the logistic equation. Suppose that this population is in fact subject to exploitation at the rate C per unit time. (For example C could be the catch of fish per year.) Then for the exploited population the logistic equation is modified to

A model including exploitation.

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - C. \tag{1}$$

In this section we will examine the implications of Equation (1) on the basis of two alternative assumptions about C: (i) that C is constant and (ii) that C is proportional to P. These alternative assumptions may be seen as corresponding to alternative strategies of exploitation.

4.1 Constant catch exploitation

In this subsection we examine the implications of Equation (1) when C is constant. This is of course an assumption about the real situation being modelled.

Assumption: C is constant

It is possible to solve Equation (1) by separation of variables. However, this requires some complicated integration and manipulation. I wish only to examine the *qualitative* behaviour of the solutions of Equation (1). This can be done more easily here by looking at direction fields than by explicitly solving the equation. In order to draw a direction field for Equation (1) it is helpful to notice that the right-hand side of the equation is a function of P only (it does not depend on t). So the slope depends only on P, not on t.

Question

What does this imply for the direction field corresponding to the Differential equation (1)?

Answer

We know that at points where the values of P are the same, the slope is the same. But the value of P is the same at points on the same horizontal line, so at such points the direction field must be parallel (see Figure 1).

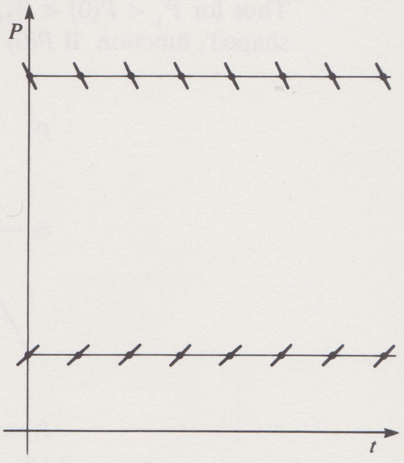


Figure 1. At points on the same horizontal line, the direction field for Equation (1) is parallel.

The slope of the direction field along each horizontal line is given by

$$\text{slope} = aP\left(1 - \frac{P}{M}\right) - C.$$

The nature of the solutions of Equation (1) depends on the size of C. It is different in character in two cases, depending on the nature of the solutions of the quadratic equation (in P)

$$aP\left(1 - \frac{P}{M}\right) - C = 0 \qquad (2)$$

Case (a) is when this equation has two real roots, case (b) when it has no real roots.

Case (a): Equation (2) has two real roots

In this case the graph of $aP\left(1 - \frac{P}{M}\right) - C$ plotted against P has the form shown in Figure 2. Since the function is a quadratic in P, the graph is a parabola. It intersects the horizontal axis at two points, which are the roots of Equation (2). I have labelled these P_1 and P_2 (where $P_1 < P_2$).

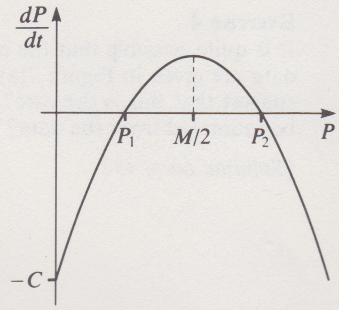


Figure 2

Figure 3 shows how we may use the graph of Figure 2, inverted and on its side for convenience, to construct the direction field for Equation (1) in this case.

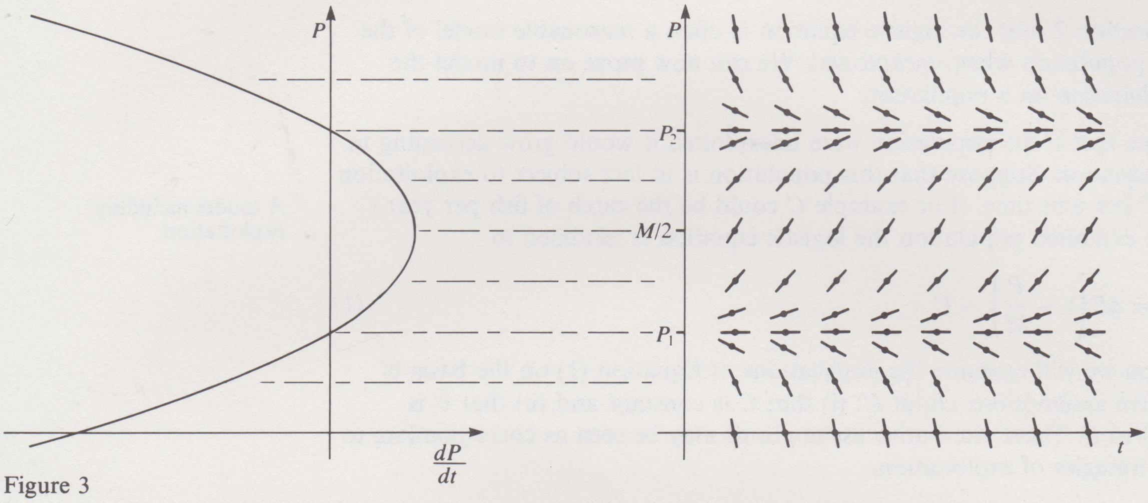


Figure 3

Question

Use Figure 3 to sketch the graph of the solution curves of Equation (1) in this case.

Answer

Figure 4 shows the required solution curves.

In this case, the slope of the solution curve is positive for P between P_1 and P_2. Thus for $P_1 < P(0) < P_2$, the solution of Equation (1) is an increasing, 'logistic-shaped', function. If $P(0)$ is outside this range, the solution is decreasing.

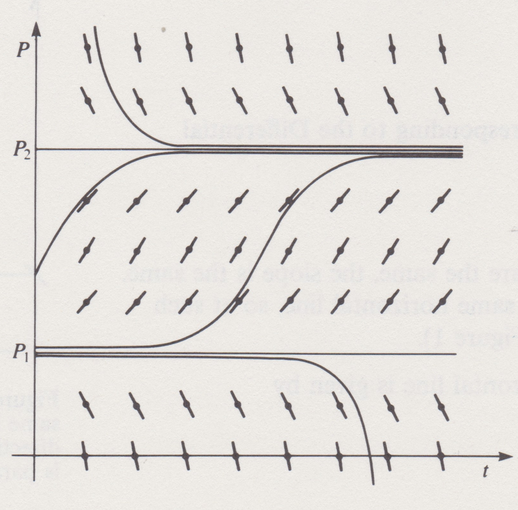


Figure 4

Case (b): Equation (2) has no real roots

Figure 5 shows the result obtained this time. In this case the slope, $aP\left(1 - \dfrac{P}{M}\right) - C$, is negative for all values of P. The solution curves are decreasing, whatever $P(0)$ is.

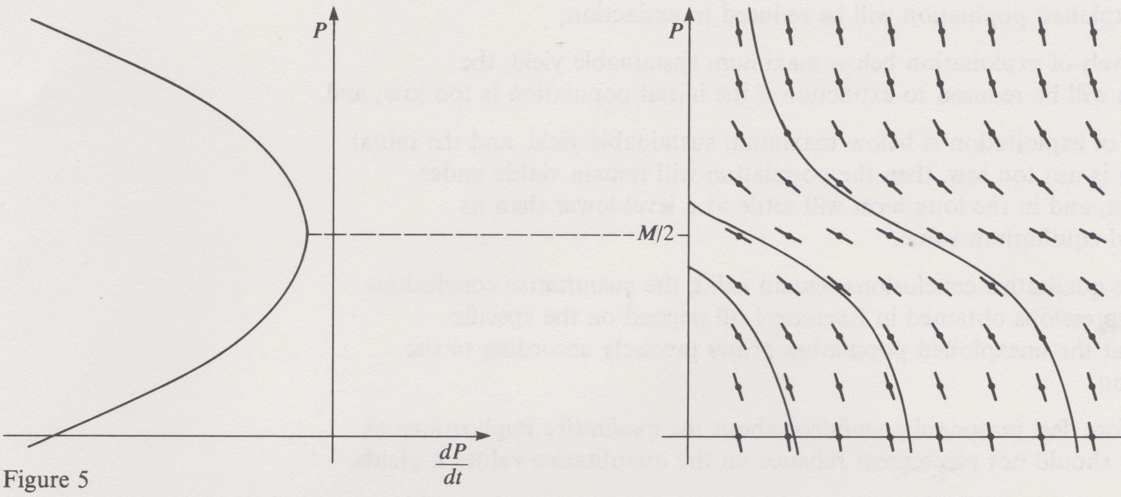


Figure 5

We now have, in Figures 4 and 5, a qualitative description of the solutions of Equation (1) when C is constant. What do these suggest about the real situation?

Qualitative implications of Equation (1)

Let us look first at the case shown in Figure 5. The model implies that, if the rate of exploitation is sufficiently high, then after the introduction of exploitation the population will consistently decrease, and eventually will fall to zero. This is in accordance with reality: too high a rate of exploitation leads to extinction.

The case described in Figure 4 is more complicated. There we are looking at the effect of a lower exploitation rate. The nature of the solutions then depends on the initial state of the population. If $P(0) < P_1$, the population decreases to extinction. If $P_1 < P(0) < P_2$, the population increases to P_2, while if $P(0) > P_2$, it falls to P_2. Thus as long as $P(0) > P_1$, the population remains viable under exploitation, and in the long term settles at P_2.

To gain the most out of exploiting the population we would like to find the *maximum sustainable yield*, that is, the maximum catch rate that can be maintained consistently without driving the population to extinction. We can readily find expressions for this and other parameters of interest in the conclusions of the model.

Quantitative implications of Equation (1)

Exercise 1

Find expressions for

(i) P_1 and P_2 in terms of a, M and C

(ii) the maximum sustainable yield in terms of a and M.

[*Solution on p. 49*]

Question

Recall that in Section 2 we saw that for many real populations the assumption made in setting up the logistic equation relating to the specific form of its right-hand side is *not* borne out in practice. What effect would deviations from this assumption have on the conclusions of the model just discussed? (Assume that a graph of dP/dt against P has the general form shown in Figure 6, rather than the specific form assumed for the logistic equation.)

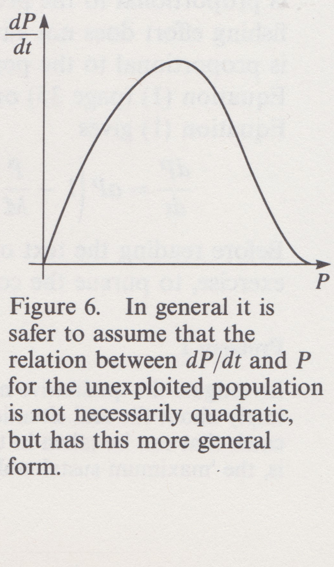


Figure 6. In general it is safer to assume that the relation between dP/dt and P for the unexploited population is not necessarily quadratic, but has this more general form.

Answer

Let us suppose that a population, when unexploited, grows in a generally logistic way, but does not follow the specific form of the logistic equation. It is reasonable to expect in general that for the unexploited population the rate of increase dP/dt

would first increase with increasing P, then, after reaching a maximum, fall again to zero, as indicated in Figure 6.

If we make only this more general assumption, the sort of direction field arguments used above will lead to the same *qualitative* conclusions. That is:

(a) if the level of exploitation is above a certain level (maximum sustainable yield) then the exploited population will be reduced to extinction;

(b) even for levels of exploitation below maximum sustainable yield, the population will be reduced to extinction if the initial population is too low; and,

(c) if the level of exploitation is below maximum sustainable yield, and the initial population is not too low, then the population will remain viable under exploitation, and in the long term will settle at a level lower than its unexploited equilibrium value.

Although these qualitative conclusions remain valid, the *quantitative* conclusions do not. The expressions obtained in Exercise 1 all depend on the specific assumption that the unexploited population grows precisely according to the logistic equation.

We can, therefore, feel reasonably confident about the *qualitative* implications of the model, but should not place great reliance on the quantitative values it yields.

It is of general importance in modelling to examine how the conclusions of a model are affected by likely variations in the assumptions made. Only those conclusions that do not change significantly under such variations are reliable.

So far we have not considered the solutions of Equation (1) for the case when the catch rate is equal to the maximum sustainable yield. This is tackled in Exercise 2, not just for Equation (1) but using the more general assumption described above.

Exercise 2

Assume that the unexploited population satisfies the equation

$$\frac{dP}{dt} = f(P)$$

where $f(P)$ has the form shown in Figure 6.

(i) Indicate on Figure 6 the maximum sustainable yield, that is, the critical rate of catch C_M above which the population is necessarily driven to extinction, but below which it is not (under suitable conditions).

(ii) Assume that exploitation takes place at the maximum sustainable yield C_M described in part (i). Use the methods of this subsection to sketch the solution curves of

$$\frac{dP}{dt} = f(P) - C_M.$$

[*Solution on p. 49*]

4.2 Constant effort exploitation

In Section 3 I noted that in fisheries models it is often assumed that the catch rate is proportional to the product of the fishing effort and the fish population. If the fishing effort does not vary with time, then this assumption implies that the catch is proportional to the population. In this section we examine the implications of Equation (1) (page 35) on this assumption. Putting $C = kP$ (k constant) in Equation (1) gives

Assumption: C is proportional to P.

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - kP. \tag{3}$$

Before reading the text of this section I would like you to try, as an extended exercise, to pursue the consequences of this model for yourself.

Problem 1

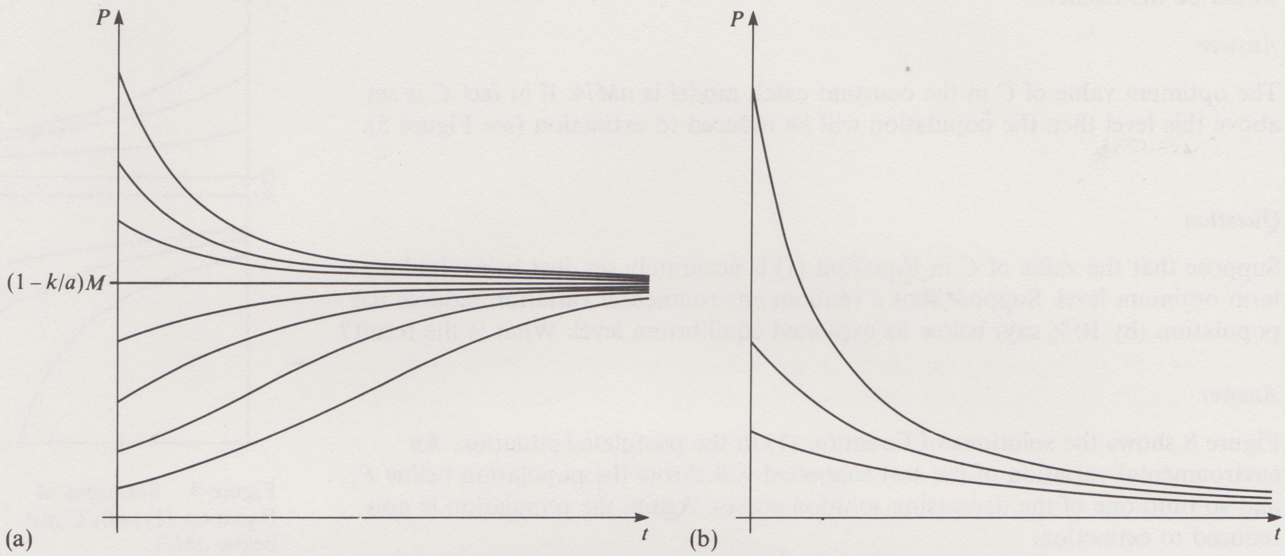
Investigate the qualitative nature of the solutions of Equation (3). What do the solutions imply about the real situation being modelled? Find an expression for the maximum rate of catch that can be taken in the long-term without driving the population to extinction (that is, the 'maximum sustainable yield'), and sketch the solutions of Equation (3) in this case.

Would your conclusions remain valid if we suppose that the relation between dP/dt and P for the unexploited population has the *general* form shown in Figure 6 rather than the specific form assumed for the logistic equation?

[*Solution on p. 52*]

I shall describe in the text only the main features of this model. The details can be found in the solution of Problem 1.

The qualitative behaviour of the solutions of Equation (3) depends on whether k is greater than or less than a. Figure 7(a) shows the solutions for $k < a$. In this case the population remains viable under exploitation (whatever the initial conditions). The long-term equilibrium level of the population is $(1 - k/a)M$.



(a) (b)

Figure 7. Solutions of the constant effort model of exploitation (Equation (3)), (a) when $k < a$ and (b) when $k > a$.

For $k > a$, the solutions of Equation (3) are decreasing whatever the initial conditions (see Figure 7(b)). The model implies that the population is eventually driven to extinction in this case.

The expression $aM/4$ for maximum sustainable yield obtained from Equation (3) is the same as that for the 'constant catch' model of Subsection 4.1 (hardly a surprise). This occurs when $k = a/2$. The solutions of Equation (3) in this case are of the general form shown in Figure 7(a).

It is advisable to look at the effect on these implications of weakening the assumption in the model that the population, if unexploited, would grow according to the logistic equation. Alternatively, we can suppose only that the unexploited population would grow according to a differential equation of the form

Effect of varying the modelling assumptions.

$$\frac{dP}{dt} = f(P)$$

where $f(P)$ has the general form indicated by Figure 6. In this case the solutions of the equation

$$\frac{dP}{dt} = f(P) - kP$$

(k constant) for the unexploited population will still be of the general form shown in Figure 7. The specific expressions obtained for the maximum sustainable yield, and for the critical values of k, are no longer valid, however.

4.3 Constant catch or constant effort?

Equation (1) with C constant may be regarded as a model of the situation in which we attempt to control exploitation by determining the *catch* taken; Equation (3) as a model of control by determining the *effort* we expend on

exploitation (the number and size of trawlers in a fishery, for example). These ideas were discussed further in the television programme, and in Section 3. Here, I wish to examine which tactic of control is theoretically preferable.

Let us accept for now that it is possible in practice to arrive at a method of estimating the optimum values for the parameters C or k in each model, but that the estimates obtained cannot be expected to be accurate. (Again, refer back to Section 3.)

Question

If the optimum value of C were overestimated in a constant catch strategy, what would be the result?

Answer

The optimum value of C in the constant catch model is $aM/4$. If in fact C is set above this level then the population will be reduced to extinction (see Figure 5).

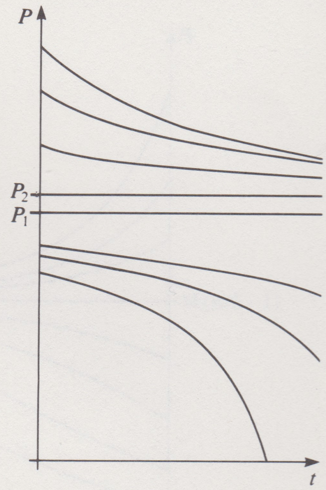


Figure 8. Solutions of Equation (1) with C just below $aM/4$.

Question

Suppose that the value of C in Equation (1) is accurately set, just below its long-term optimum level. Suppose that a random environmental variation reduces the population (by 10% say) below its exploited equilibrium level. What is the result?

Answer

Figure 8 shows the solutions of Equation (1) in the postulated situation. An environmental variation of the sort suggested will throw the population below P_1, and so onto one of the decreasing solution curves. Again, the population is now reduced to extinction.

The sort of considerations described in these questions lead me to describe the constant-catch strategy as **unstable**. In practice, it will only be safe to take the same constant catch year after year if the catch is set well below its optimum level.

The constant catch strategy is unstable.

Let us now examine the stability of the constant effort strategy.

Question

What happens if the optimum value of k in Equation (3) is estimated somewhat inaccurately, or if environmental variations reduce the population below the exploited equilibrium level in a constant effort strategy?

Answer

The solutions for the optimal constant effort strategy with $k = a/2$ in Equation (3), are shown in Figure 9. If the population is reduced from its equilibrium level by some random factor, it will return to that level. If the value of k is set a little above, or below, its optimum value, the picture of the solutions is much the same.

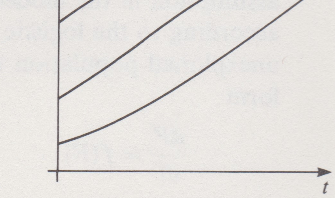


Figure 9. Solutions of Equation (3) with $k = a/2$.

There is no danger of extinction if k is set a little inaccurately; the only effect is that exploitation will be a little less than optimum. We may describe the constant effort strategy as **stable**.

The constant effort strategy is stable.

Question

Are the above stability arguments dependent on the specific form of the right-hand side of the logistic equation?

Answer

No. The qualitative arguments can be carried through so long as the relation between dP/dt and P is of the general form shown in Figure 6.

The implications of these results for the practical control of fisheries (discussed in Section 3) are interesting, but not straightforward. Fisheries scientists set quotas on the catch because they are unable in practice to exercise direct control over the level of fishing effort. However, their quotas on catch are calculated on the basis of the same level of fishing effort from year to year. So they attempt to attain a 'constant effort' strategy of exploitation, but have to do this through quotas on catch.

It is my own feeling that the results above show that any attempt at control through quotas on catch holds dangers. I see the results above as showing not so much the superiority of 'constant effort' over 'constant catch' in this situation, but rather that any attempt at control through the catch is liable to instability.

Summary of Section 4

In this section the implications of a model of exploitation were examined. If we assume that, when unexploited, the population grows according to the logistic equation, and that the population is exploited at a rate C, then growth of the exploited population P with time t is given by

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - C \qquad (1)$$

The solutions of this equation were examined in two cases:

(I) C constant (constant *catch*)

(II) C proportional to P (constant *effort*).

In case (I), the qualitative conclusions of the model are

(a) that if the level of exploitation is above a certain level (maximum sustainable yield), then the exploited population will be reduced to extinction;

(b) that even for levels of exploitation below maximum sustainable yield, the population will be driven to extinction if the initial population is too low; and

(c) if the level of exploitation is below maximum sustainable yield, and the initial population is not too low, then the population will remain viable under exploitation and in the long term will settle at a level lower than its unexploited equilibrium value.

In Case (II), the qualitative conclusions are somewhat different.

(a) If the effort exerted is above a certain level, then the population will be driven to extinction.

(b) If the effort is below the crucial level mentioned in (a) then the population remains viable under exploitation whatever the initial conditions.

(c) The optimum level of effort, for maximum catch, is substantially less than the level of effort causing extinction. (Half of it, if we take the model literally.)

The implications of replacing the term $aP\left(1 - \dfrac{P}{M}\right)$ with a similar, but more general, term $f(P)$ were also examined. Reliance can only be placed on those conclusions of the model that are not greatly changed by such a change in the assumptions of the model. The qualitative conclusions above are not affected by this change.

Certain quantitative conclusions, in particular that the maximum sustainable yield is $aM/4$, were drawn from the models. However these are less reliable than the qualitative conclusions, as they depend on the precise form of the logistic equation.

The **stability** of the 'constant effort' and 'constant catch' strategies that give maximum catch was discussed. It was noted that the constant catch strategy is unstable, but that the constant effort strategy is stable.

End of section exercise

Exercise 3

A population of a species of edible turtle is discovered on an uninhabited island. Biologists are able to arrive at an estimate of M (the equilibrium population level) and a (the maximum proportionate rate of increase of which the population is capable). It is proposed to exploit the population, and to set an annual quota of $aM/4$ turtles.

What are your comments on this procedure? Is there a preferable alternative?

[*Solution on p. 50*]

5 End of unit problems

Problems 1 to 3 below (together with Problem 1 of Section 2 and Problem 1 of Section 4) are intended to give you the opportunity to try some extended problems with a 'modelling' content. The problems below can be expected to take a fairly long time (particularly Problem 2), so you may not have time to try them all. These problems are not routine exercises on the preceding text. They are included partly as an aid in preparing for the course project (perhaps 'getting in the right frame of mind' would be more appropriate than 'preparing') and also because as the course develops, if not now, you may want some more substantial problems to try.

Problem 4 is rather different, as it is essentially a 'theoretical' exercise. It relates the ideas in Section 3 to those in Section 2. It is more difficult than anything you would be expected to do for assessment and so is 'optional'.

Problem 1

For some bird populations the key factor limiting growth is the number of young that can be reared in the nesting area of the population.

(i) Construct a recurrence relation model of the growth of such a population near equilibrium, based on the two assumptions:

(I) that the annual number of births is constant

(II) that the annual number of deaths is a constant *proportion* of the population.

(ii) Solve your recurrence relation from (i) and sketch a graph of the solutions.

(iii) Could this model be appropriate for the growth of a population starting from a low level? Are there any circumstances under which this model might give similar results to the logistic model?

(iv) Table 4 gives data on a hypothetical population. Use this to calculate the annual number of deaths, and to test the accuracy of the proposed assumptions (I) and (II) for this population. Which of the following would be a reasonable way of using this model?

(a) To estimate the population in 1960.

(b) To predict the population in 1990.

(c) To estimate the equilibrium level for this population.

(d) To estimate when the population will be within 5% of its equilibrium level.

(e) To estimate when it will be within 0.5% of its equilibrium level.

Perform those calculations of (a)–(e) that are appropriate uses of the model.

[*Solution on p. 53*]

Year	Total population (hundreds)	Number of juveniles (hundreds)
1970	699	99
1971	729	104
1972	758	101
1973	780	96
1974	800	102
1975	824	97
1976	840	99

Table 4. Hypothetical population data. The data are obtained in the autumn of each year, at the end of the breeding season, while juveniles (birds born in the year concerned) are still recognizable.

Problem 2

This problem concerns a laboratory experiment on the exploitation of a population of guppies. Populations of these fish were maintained in aquaria. In one case the growth of the unexploited population was observed (see Figure 1(a)); in the other a set percentage of the population was removed every three weeks, to simulate 'harvesting' (see Figure 1(b)). Once a week the biomass of each population was measured. The unexploited population grew to a fairly steady equilibrium level of 32 grams.

The equilibrium levels of the exploited population varied according to the rate of exploitation. When 10% were removed every three weeks the population stabilized at about 23.5 grams, while at an exploitation rate of 25% per three weeks the stable population level was 15 grams. The results for exploitation rates of 50% and 75% are also shown below. Estimate the maximum sustainable yield from this population.

In a modelling problem such as this there are 'better' and 'worse' answers but there is no single 'right' answer.

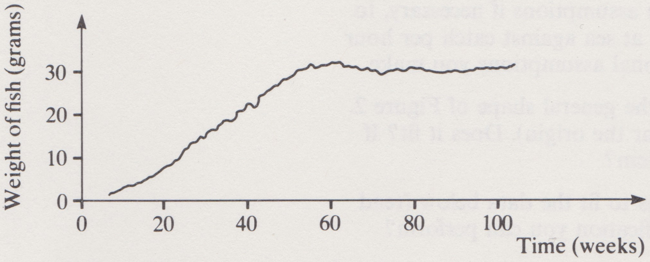


Figure 1(a). Weekly measurements of an unexploited guppy population.

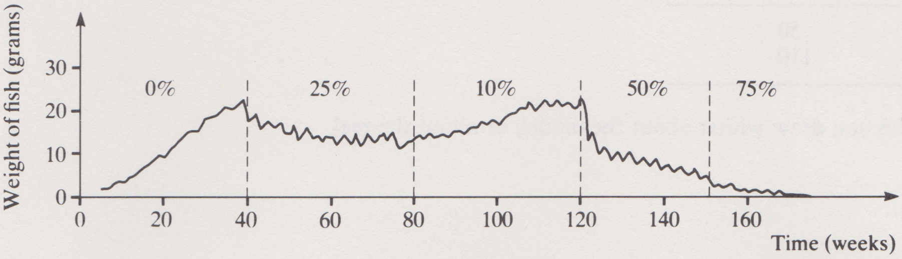


Figure 1(b). Weekly measurements of a guppy population exploited at three weekly intervals at the rates indicated.

What exploitation rate would you recommend if this were a practical fishery situation (such as, for example, a fish farm).

[*Solution on p. 54*]

Problem 3

This problem concerns a difficulty that arises in the quantification of 'fishing effort'. Two possible measures of this are

(I) (weight of each trawler) × (number of days at sea)

(II) (weight of each trawler) × (number of hours actually fishing),

summed over the vessels involved during the year. Figure 2 shows data relating the catch per day at sea to the catch per hour actually fishing, for various trawlers.

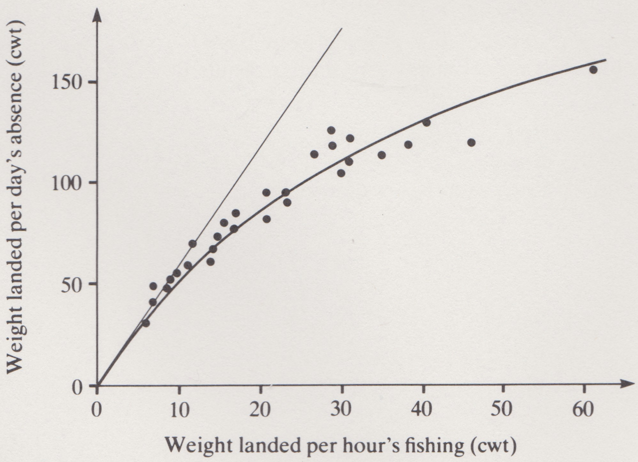


Figure 2

Since these two quantities are not proportional to each other, the measures of fishing effort proposed above are not equivalent.

(i) If we are to have the catch proportional to fishing effort times fish population, which measure of 'fishing effort' is more likely to be satisfactory?

(ii) We may construct a model to explain the relationship shown in Figure 2 as follows.

Suppose that a trawler has a hold that will contain X tons of fish. Suppose also that on any particular trip the trawler stays on the fishing grounds long enough to fill the hold, so that the only thing that varies from trip to trip is the time that this takes. This time may be seen as the sum of (1) a fixed time, required to travel to and from the fishing grounds, and for 'processing' the fish caught and (2) a variable time, dependent on the abundance of fish in the fishing grounds.

(a) Use this framework, together with other reasonable assumptions if necessary, to predict the shape of a graph plotting catch per day at sea against catch per hour actually fishing (for various trips). Note any additional assumptions you make.

(b) Compare the shape predicted by your model with the general shape of Figure 2. (Look in particular at the gradient of the graph near the origin). Does it fit? If not, can you modify your model to avoid the problem?

(c) Can you choose the parameters in your model so as to fit the data below (read from Figure 2). If you can, is there any further verification you can perform?

Weight/hour fishing	Weight/day at sea
10	50
30	110

(d) What conclusion (if any) can you draw (either about the model, or about the real situation)?

[*Solution on p. 55*]

Appendix 1

Solutions to the exercises in Section 1

1. Let P_n denote the population n three-month periods after January 1960. The initial population is 100, and the number of deaths in each three-month period is half of the population at the beginning of the period. Thus

$$P_0 = 100 \text{ and } c = 0.5.$$

To find b, I will assume that half the population is female, and interpret the phrase 'average breeding success of a female rabbit' to mean that the given figure takes into account the fact that some of the females may be immature and others infertile or too old. Making these assumptions:

$$\text{births} = 2 \times (\tfrac{1}{2}P_n)$$

i.e. $b = 1$.

Hence we have from Equation (7) in the text

$$\begin{aligned} P_n &= (1 + 1 - \tfrac{1}{2})^n \times 100 \\ &= 100(\tfrac{3}{2})^n. \end{aligned}$$

(Use of Equation (7) implicitly assumes that (a) there is no migration, (b) births and deaths remain a constant proportion of the population.)

The realism of this prediction is discussed at the beginning of the next subsection.

2. The logarithms of the data in Table 1 are plotted in Figure 8(a) in the text. The graph obtained looks reasonably linear, and so an exponential model fits the data fairly well. (This is discussed further in the text.)

A linear equation fitting the data points fairly well is given below. I have not calculated the least squares fit, so your answer may be a little different. I got

$$z = 1.8 + 0.93t$$

where z is the $\log_e$ of the population t years after 1955. To obtain an equation giving P in terms of t, we take exponentials:

$$P = 6.05e^{0.93t}.$$

This result is unlikely to be accurate to more than one significant figure, so it is best quoted as

$$P = 6e^{0.9t}.$$

3. (i) Major assumptions made in constructing the model were:

(I) annual births and annual deaths are each proportional to the population at the start of the year, and

(II) there is no significant migration or exploitation.

Examples of factors not taken into account by (I) are:

(a) the balance of males and females in the population;

(b) the balance of the population by age;

(c) variations in environmental conditions from year to year.

Obviously the model does not take migration or exploitation into account!

Other assumptions were made in constructing the model, for example that 'population' may take any positive value (whereas it clearly must in fact be an integer). Also population changes were only considered in distinct, equal time periods; in practice they may occur at any time. Such technical choices inevitably need to be made in setting up a mathematical model. It seems unlikely that they will have a significant effect on the model, but even here one should be careful, for they can do.

(ii) (a) In each of these examples the population grows rapidly to begin with, then growth levels off and stops. In each case births and deaths may be proportional to the population in the first part of the time period, but they cannot remain a set proportion, for there are more births than deaths at the beginning while by the end there are equal numbers of births and deaths. Either the proportion of births has decreased or the proportion of deaths has increased. It seems quite reasonable that as a population increases in density, individuals begin to find it difficult to find sufficient food, and so the proportion of deaths might well increase. (This type of population variation is discussed at length in Section 2.)

(b) Evidently in this case the idea that births and deaths are each a set proportion of the population breaks down entirely. Presumably the number of births and/or deaths is largely dependent on the state of various environmental factors—that seem to vary greatly—and perhaps are not particularly dependent on the actual population size. (There evidently must be some relation between births and deaths and population size. The population must be non-zero for there to be any births! However, if individual moths lay many eggs then it may be that in favourable conditions a very small population can produce a large number of births.)

4. (i) *Box 4: Solve the mathematical problem.*

$$\frac{dP}{dt} = (B - C)P$$

You may immediately recognize that the solution of this differential equation is

$$P = P_0 \exp((B - C)t).$$

If not, it can be solved by separation of variables, as follows.

$$\frac{1}{P}\frac{dP}{dt} = B - C$$

so

$$\int \frac{dP}{P} = \int (B - C)\,dt$$

hence $\log_e P = (B - C)t + K$

where K is an arbitrary constant. Hence

$$\begin{aligned} P &= \exp K \exp((B - C)t) \\ &= P_0 \exp((B - C)t). \end{aligned}$$

Here $P_0 (= \exp K)$ is an arbitrary constant. I have written it as P_0 because $P = P_0$ when $t = 0$ that is, P_0 is the 'initial' size of the population.

Boxes 5 and 6: Interpret the solution and compare with reality

These steps are essentially the same as the discussion of Equation (7) on page 13 (Box 5) and page 14 (Box 6) because we again have an exponential model

(ii) The major difference lies in the process of population change being considered as one that is continuous in time, rather than partitioning time into discrete periods and considering only changes from one period to the next.

For most naturally occurring populations the year provides a natural time period to work with, and variations in population within a year have little to do with the exponential model. In this case the recurrence relation formulation is preferable.

For some populations, particularly in laboratory experiments, in which births and deaths may occur at any time and there is no natural basis on which to choose a time period, the differential equation would seem more realistic.

5. (i)

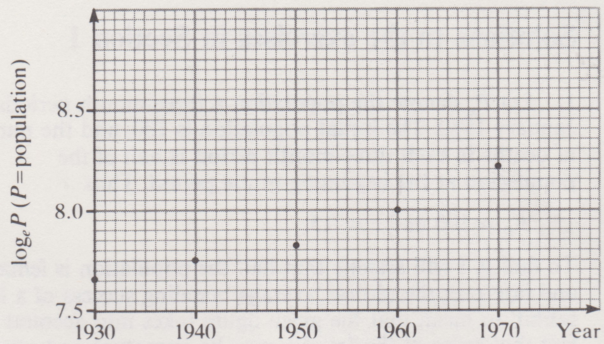
$$\begin{pmatrix}\text{Increase in bank}\\ \text{balance during}\\ \text{period.}\end{pmatrix} = \begin{pmatrix}\text{Deposits plus}\\ \text{interest during}\\ \text{period.}\end{pmatrix} - \begin{pmatrix}\text{Withdrawals}\\ \text{plus charges}\\ \text{during}\\ \text{period.}\end{pmatrix}$$

(ii)

$$\begin{pmatrix}\text{Increase in}\\ \text{quantity}\\ \text{of water}\\ \text{in reservoir.}\end{pmatrix} = \begin{pmatrix}\text{Inflow (from}\\ \text{rivers etc.)}\\ \text{plus rainfall.}\end{pmatrix} - \begin{pmatrix}\text{Outflow plus}\\ \text{evaporation.}\end{pmatrix}$$

I am interpreting 'outflow' here as covering outflow in rivers (if any) and water extracted through pipes and any 'leakage'; you may have introduced these ideas separately.

6. The figure shows a plot of the logarithms of the data in Table 2.



A straight line would provide some sort of fit to the points, indicating that exponential growth provides a general picture of this population. The points in fact show a tendency to curve upwards. This indicates that the difference between births and deaths as a proportion of the population is increasing—so either the proportionate birth rate is increasing, or the proportionate death rate falling, or both. Without further information, the best short-term extrapolation might be provided by fitting a straight line to the last three data points.

Solutions to the exercises in Section 2

1. (i) The differential equation

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right)$$

may be solved by separation of variables (see *Unit 2*, Section 3). We have

$$\int \frac{dP}{P\left(1 - \dfrac{P}{M}\right)} = \int a\,dt + C$$

$$= at + C$$

where C is an arbitrary constant.

We can evaluate the integral on the left using partial fractions.

$$\int \frac{dP}{P\left(1 - \dfrac{P}{M}\right)} = \int \left(\frac{1}{P} + \frac{1}{M - P}\right) dP$$

$$= \log_e P - \log_e (M - P)$$

$$(\text{since } 0 < P < M)$$

$$= \log_e \left(\frac{P}{M - P}\right).$$

Hence the general solution of the differential equation is given implicitly by

$$\log_e \left(\frac{P}{M - P}\right) = at + C.$$

Taking exponentials we obtain

$$\frac{P}{M - P} = \exp(at + C) \qquad (1)$$

and rearranging gives

$$P = e^{at+C}(M - P)$$

so $\quad Pe^{-(at+C)} = M - P$

hence $P(1 + e^{-(at+C)}) = M.$

So the general solution is

$$P = \frac{M}{1 + e^{-(at+C)}}$$

where C is an arbitrary constant.

(ii) We can most easily find the value of C corresponding to the initial condition $P = P_0$ when $t = 0$ by returning to Equation (1) above. When $t = 0$ this gives

$$\frac{P_0}{M - P_0} = e^C.$$

Hence $e^{-C} = \dfrac{M - P_0}{P_0} = \dfrac{M}{P_0} - 1$ and putting this in the general solution gives the required particular solution

$$P = \frac{M}{1 + \left(\dfrac{M}{P_0} - 1\right)e^{-at}} \qquad (0 < P_0 < M).$$

2. (i) If t is large and positive, then e^{-at} is very nearly zero. Hence in this case $P \simeq M$. (Stated formally, P converges to M as t tends to infinity.)

(ii) If t is large and negative, then e^{-at} is very large. So in this case P is very close to zero.

(iii) If $0 < P_0 < M$ then $\dfrac{M}{P_0} > 1$, so $\dfrac{M}{P_0} - 1 > 0$. Hence P equals M divided by a number larger than 1, so $0 < P < M$.

(iv) Looking at the differential equation

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right)$$

we have, from (iii), that $P > 0$ and $1 - \dfrac{P}{M} > 0$ (since $P < M$); also $a > 0$. Hence $dP/dt > 0$ for all values of t. Thus the solution curve must be increasing for all values of t.

We now have sufficient information to sketch the graph of Equation (4) when $0 < P_0 < M$. This is done in Figure 2(a) in the text.

(v) The solution corresponding to the initial condition $P = P_0'$ is

$$P = \frac{M}{1 + \left(\frac{M}{P_0'} - 1\right)e^{-at}}.$$

If a number α is chosen so that

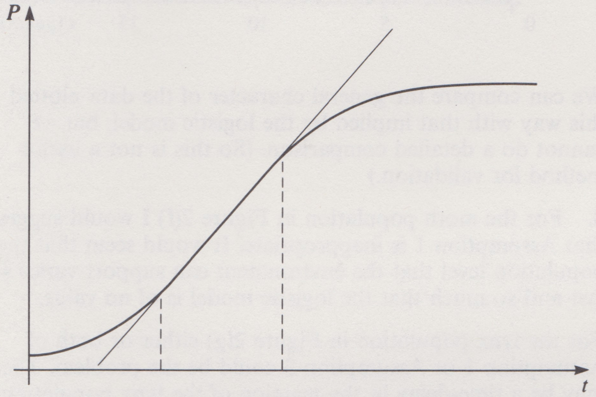
$$\left(\frac{M}{P_0'} - 1\right) = \left(\frac{M}{P_0} - 1\right)e^{a\alpha}$$

then the above solution can be written

$$P = \frac{M}{1 + \left(\frac{M}{P_0} - 1\right)e^{-a(t-\alpha)}}$$

which is the solution corresponding to the initial condition $P = P_0$ shifted α units along the t axis.

3. Just going by eye, the central part of the logistic curve between the dotted lines looks approximately linear.



So approximately linear population increase, over a limited period of time, and in certain circumstances, is implied by the logistic model. (Just as exponential growth is, with similar caveats.) For a population that is around half its equilibrium value, and for extrapolation over a fairly short period of time, a linear model would produce similar results to a logistic model.

4. (i) Equation (6) is the logistic equation rearranged in the form

$$\left(\frac{M}{P_0} - 1\right)e^{-at} = \frac{M}{P} - 1.$$

In this case we have $P = P_n$ when $t = n$, so

$$\left(\frac{M}{P_0} - 1\right)e^{-an} = \frac{M}{P_n} - 1,$$

and, since $P = P_{n+1}$ when $t = n + 1$,

$$\left(\frac{M}{P_0} - 1\right)e^{-a(n+1)} = \frac{M}{P_{n+1}} - 1.$$

If we divide the first of these equations by the second, we obtain

$$\frac{e^{-an}}{e^{-a(n+1)}} = \frac{\frac{M}{P_n} - 1}{\frac{M}{P_{n+1}} - 1}.$$

The left-hand side of this equation is just e^a, so multiplying by $\frac{M}{P_{n+1}} - 1$ gives

$$e^a\left(\frac{M}{P_{n+1}} - 1\right) = \frac{M}{P_n} - 1,$$

as required.

(ii) The equation in (i) can be rearranged as follows

$$e^a(M - P_{n+1}) = M\frac{P_{n+1}}{P_n} - P_{n+1};$$

so $$\frac{P_{n+1}}{P_n} = \left(\frac{1 - e^a}{M}\right)P_{n+1} + e^a;$$

i.e.

$$\frac{P_{n+1} - P_n}{P_n} = \left(\frac{1 - e^a}{M}\right)P_{n+1} + (e^a - 1).$$

(iii) The straight line has equation

$$\frac{P_{n+1} - P_n}{P_n} = \left(\frac{1 - e^a}{M}\right)P_{n+1} + (e^a - 1).$$

It intersects the P_{n+1} axis when $\left(\frac{1 - e^a}{M}\right)P_{n+1} + (e^a - 1) = 0$, that is, when

$$P_{n+1} = M.$$

It intersects the $(P_{n+1} - P_n)/P_n$ axis when $P_{n+1} = 0$, that is, when

$$\frac{P_{n+1} - P_n}{P_n} = e^a - 1.$$

(iv) The data in Figure 6(a) are well-fitted by a straight line, except that the earlier points are rather scattered. This method of plotting certainly makes the fit look a good deal worse than does the method used before (see Figure 5). Small deviations of data from the logistic form are exaggerated by this method of plotting. Having made this observation, the data in Figure 6(b) also seem adequately linear. They are scattered, but there is no indication of any specific non-linear trend. The data in Figure 6(c) are suspicious. We can draw a straight line fairly close to all these points, but the points are much better fitted by a nonlinear curve than by a straight line. This is discussed later in Subsection 2.5.

(v) The straight line intersects the P_{n+1} axis at $\frac{1.0396}{0.0018433}$ and the $(P_{n+1} - P_n)/P_n$ axis at 1.0396 so from (iii) we have

$$M = \frac{1.0396}{0.0018433}$$
$$= 564 \text{ (to 3 significant figures)},$$

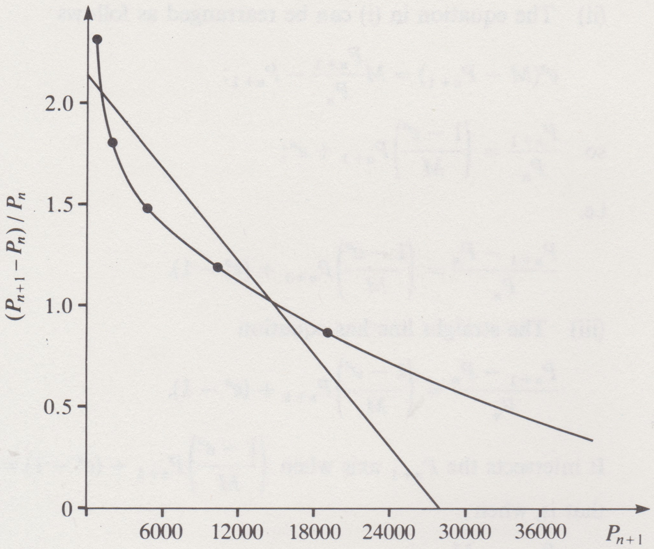
and $e^a - 1 = 1.0396$, so

$$a = \log_e(2.0396)$$
$$= 0.713 \text{ (to 3 significant figures)}.$$

Despite the scatter in Figure 6(b), the estimate obtained for M seems very reasonable. The estimate for a is more dependent on the scattered, earlier, data points near the $(P_{n+1} - P_n)/P_n$ axis intercept, and so is likely to be less accurate.

5. For the data in Table 1(b), this seems a reasonable procedure. There is data available for the whole range of population sizes, up to and around equilibrium, so that the best fit straight line is constrained by data near equilibrium. Secondly, it seems reasonable to fit a straight line to this data. It is scattered, but shows no consistent trend away from linearity. In fact, this procedure was adopted in the solution to Exercise 4, and the result obtained there looked reasonable.

For the data in Table 1(c) this is wholly unreasonable. The data plotted in Figure 6(c) shows a non-linear trend and so it would be more sensible to calculate the equilibrium population M using a curve rather than a straight line.



If we assume $g(P)$ has the form of the curve shown above then the equilibrium population M occurs where the curve intersects the P_{n+1} axis, for then $g(P)$, and hence $\frac{dP}{dt}$, is zero (this generalizes the result in Exercise 4 where $g(P)$ was assumed to be linear). We cannot obtain a definite estimate of M from the curve, as I have not been able to extend it to cut the horizontal axis on the scale given. However, it is clear that an estimate of M obtained this way will be of a different order of magnitude from that obtained using the straight line. The use of the straight line is no more than a reiteration of Assumption (2) made in setting up the logistic equation, and this assumption is not universally supported by data. There are no theoretical grounds for preferring the straight line; there are empirical grounds for preferring the curve; and the results they give are quite different, even in terms of the sort of accuracy we might expect in population studies such as this.

Conclusion: the procedure proposed will yield nonsense in this case.

6. (i) If we have data on the growth of a population P_n at equal time periods, then Assumption (2) suggests that a plot of $(P_{n+1} - P_n)/P_n$ against P_{n+1} (or P_n) should be linear.

(ii) Construct a suitable laboratory experiment, to measure directly the proportionate growth rate of a population at different population levels (see Figure 8 of Section 2).

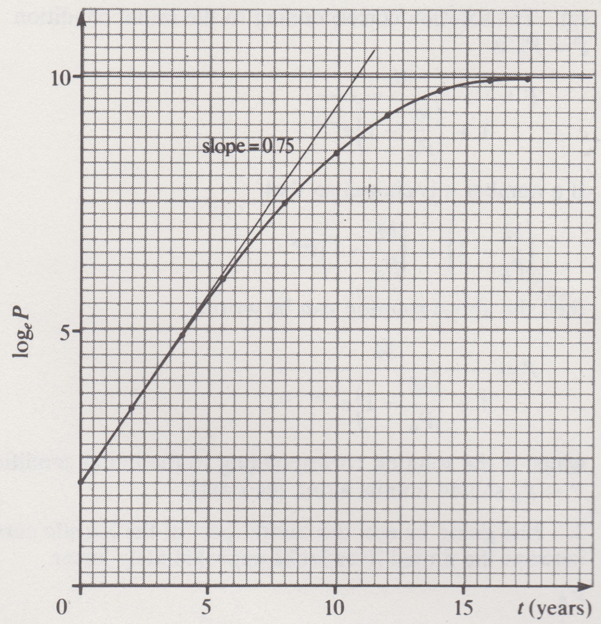
7. For exponential growth, the proportionate growth rate is constant, a graph of $\log_e P$ against t is linear, and the gradient of the straight line equals the proportionate growth rate. For logistic growth the proportionate growth rate decreases as t increase. The parameter a is the proportionate growth rate at low population levels.

In the given plot of $\log_e P$ against t, the slope of the curve does decrease with time, thus agreeing with the general character of the implications of the logistic model. To estimate a, we can look at the slope of the curve at low population levels. The figure shows a straight line drawn for this purpose giving $a = 0.75$.

The horizontal line is used to estimate M:

$$\log_e M \simeq 10,$$

so $M \simeq 22000$.

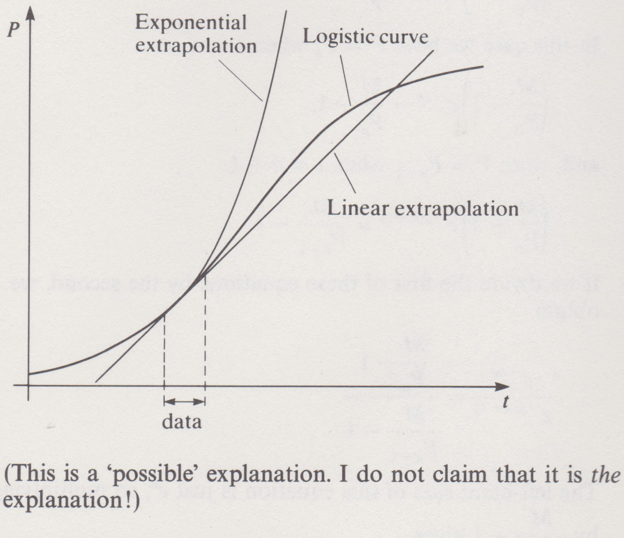


We can compare the general character of the data plotted this way with that implied by the logistic model, but we cannot do a detailed comparison. (So this is not a useful method for validation.)

8. For the moth population in Figure 2(f) I would suggest that Assumption 1 is inappropriate. It would seem that the population level that the environment can support varies so fast and so much that the logistic model is of no value.

For the lynx population in Figure 2(g) either or both of Assumption 1 or Assumption 3 could be the problem. There may be a time-delay in the reaction of the lynx population to changes in its level, leading to oscillations in population size for the sort of reasons described qualitatively in the text (page 27). Alternatively, the equilibrium lynx population could be oscillating systematically, because of some interaction elsewhere in the ecosystem.

9. Were the data provided from a logistic curve (say from the part between the dotted lines in the figure), then it could be well fitted by an exponential, but linear extrapolation would be more accurate.



(This is a 'possible' explanation. I do not claim that it is *the* explanation!)

Solutions to the exercises in Section 3

1. The main problem is the fact that recruitment (annual births) is not a well-determined function of population at all. It depends on population, but there is also a great deal of variation from year to year not accounted for by variations in population size.

2. From Figure 7(b) we see that when $f = 0$, $\frac{Y}{f}$ is about 12. The straight line cuts the horizontal axis at $f = 64$. So, assuming a linear relationship,

$$\frac{Y}{f} = 12 - \frac{12}{64}f$$

thus

$$Y = 12f\left(1 - \frac{f}{64}\right).$$

This quadratic is a maximum at $f = 32$. So the maximum sustainable yield is

$$12 \times 32 \times \left(1 - \frac{32}{64}\right) \text{ (units)}$$
$$= 192 \text{ (units)}.$$

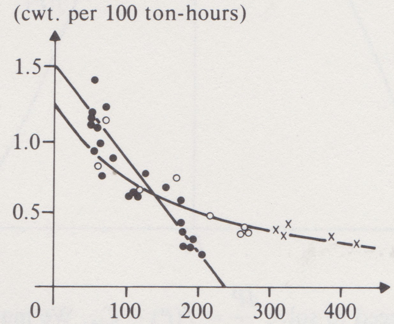
The optimum level of fishing effort is 32 (units).

This calculation uses assumptions (ii) and (iii) in the summary of Section 3. It also assumes that the relationship between Y/f and f is linear, and that the straight line shown in Figure 7(b) is the most appropriate straight line to use.

Another reasonable method, which you might have used, would be to fit a curve rather than a straight line to the data and compute the maximum sustainable yield accordingly; this method should not produce substantially different results in this case.

3. (i) When the population is above the level at which the sustainable yield is maximum.
(ii) When the population is below the level at which the sustainable yield is maximum.

4. The data do rather suggest that the conditions underlying the fishery have changed. On the figure below I have drawn (just by eye) a straight line fitting the data for 1907–38, together with a curve fitting the data for 1947–58. These look very different, suggesting a change either in the ecology of the stock, or in fishing methods.



Assuming there has been such a change, it would seem sensible to use only the more recent data in estimating the appropriate level of fishing under current conditions. One could, for example, use the curve in the figure, and construct from it a curve of Y against f, and so find (approximately) the level of effort for which Y is maximum.

An alternative (but similar) procedure would be to fit a straight line to the data for 1947–58, or possibly to just the data for 1954–58. This would give Y/f as a linear function of f—say $Y/f = r + sf$. We would then need to find the value of f for which $Y = f(r + sf)$ is maximum.

Solutions to the exercises in Section 4

1. (i) P_1 and P_2 are the solutions of the quadratic equation, in P,

$$aP(1 - P/M) - C = 0. \qquad (1)$$

In standard form this equation is

$$\frac{a}{M}P^2 - aP + C = 0.$$

Its solutions are

$$P = \frac{M}{2a}\left(a \pm \sqrt{a^2 - 4\frac{aC}{M}}\right)$$
$$= \frac{M}{2}\left(1 \pm \sqrt{1 - \frac{4C}{aM}}\right).$$

Since $P_1 < P_2$, we have

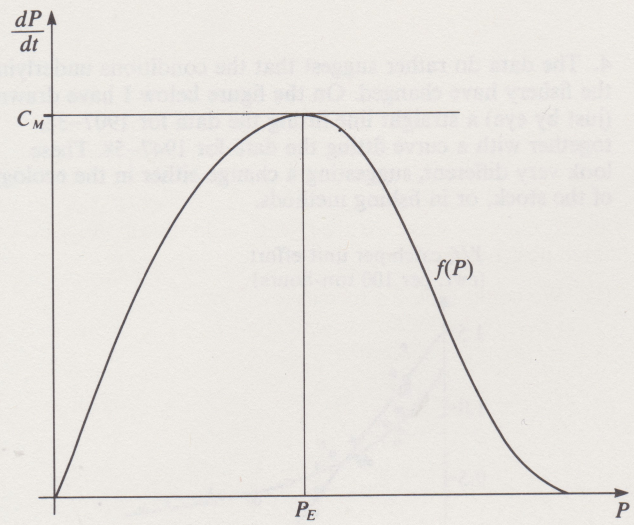
$$P_1 = \frac{M}{2}\left(1 - \sqrt{1 - \frac{4C}{aM}}\right)$$
$$P_2 = \frac{M}{2}\left(1 + \sqrt{1 - \frac{4C}{aM}}\right).$$

(ii) The population can remain viable under exploitation so long as equation (1) has real roots. This occurs if $\sqrt{1 - \frac{4C}{aM}}$ is real; that is, if $\frac{4C}{aM} \leq 1$, or

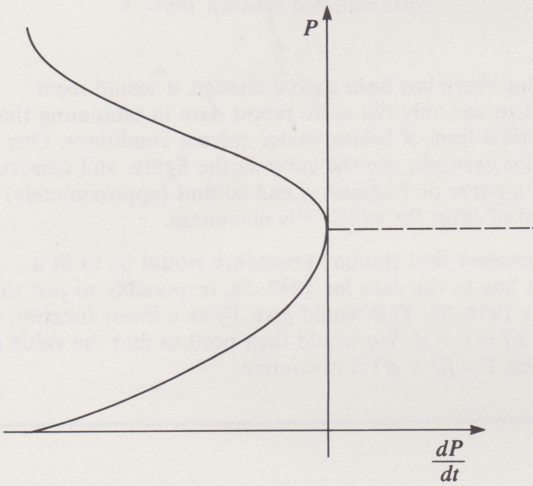
$$C \leq \frac{aM}{4}.$$

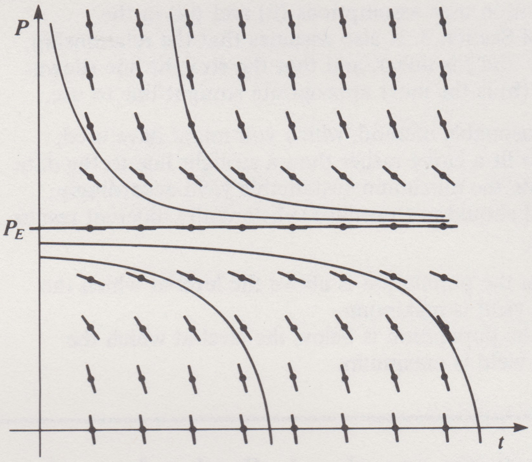
The case when C is actually equal to $\frac{aM}{4}$ has not been discussed in the text, but it is covered in Exercise 2. The population is certainly viable for any exploitation rate up to $\frac{aM}{4}$, according to the model, so we can say that the 'maximum sustainable yield' according to the model is $\frac{aM}{4}$.

2. (i) The equation for the exploited population is $\frac{dP}{dt} = f(P) - C$ and so the population will fall to zero unless $f(P) - C \geq 0$ for some P. C_M is shown in the figure; it is the maximum value of C for which $f(P) - C \geq 0$ for some P.



(ii) We need to solve $\frac{dP}{dt} = f(P) - C_M$. We may use the graph of $f(P) - C_M$ against P (on its side) to draw the direction field and sketch the solution curves as shown below (compare with Figure 5 of the text).





3. I would make the following comments:
(a) Presumably a and M cannot be estimated with total confidence, and anyway will be subject to some variation from year to year.

(b) The expression $aM/4$ depends on the assumption that when unexploited the population would grow according to the logistic equation. Without empirical verification of this, the expression $aM/4$ must be treated with extreme caution.

(c) The 'constant catch' strategy proposed is inherently unstable. If the quota set is too high, and there are reasons to anticipate this possibility (see (a) and (b)), then the population will be driven to extinction if the same quota is taken each year.

If this quota *is* set, it is crucial to monitor population levels, and to stop (or drastically reduce) exploitation if the population falls below half its unexploited equilibrium level. (Since this should be the equilibrium level of a 'properly' exploited population.)

A safer strategy would be to take a set *proportion* of the turtle population each year. The quota could be set at a proportion $a/2$ of the population, as suggested by the 'constant effort' strategy. This procedure is unlikely to lead to extinction, although for optimum exploitation it would be advisable to collect further biological data since, in practice, $a/2$ might not be the proportion giving maximum yield.

Appendix 2

Solution to the problem in Section 2

1. This is a very open-ended question, and there is no 'right' answer. I will deal with the two specific suggestions first, then mention other possible lines of further investigation.

(i) If the environment varies with time, then the equilibrium population M varies with time. A natural way to allow for this is to make M in the logistic equation a function of t:

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M(t)}\right).$$

In pursuing such a model, one might investigate the consequences of inputting various functions for $M(t)$. One might well wish to incorporate statistical ideas, but I do not want to discuss that possibility here.

(ii) To allow for a time-delay, one might assume that the proportionate growth rate at time t depends on the population at an earlier time, say $t - \tau$ (where τ is a fixed constant). Assuming this, and otherwise adopting the assumptions of the logistic model, leads to the equation

$$\frac{dP(t)}{dt} = aP(t)\left(1 - \frac{P(t-\tau)}{M}\right).$$

This is not a mathematical formulation that is easy to handle, however. (It is a 'delay-differential' equation.)

An alternative way of effectively building in a time-delay is to set up a recurrence relation model. If we assume that the proportionate increase in population during each time interval declines linearly with the population at the *start* of the interval, then we arrive at the recurrence relation

$$P_{n+1} - P_n = aP_n\left(1 - \frac{P_n}{M}\right)$$

for the population P_n after n equal time periods.

There are various other ways we could proceed further. (Which way is appropriate, or whether we want to do so at all, depends on what we are trying to do.) I will describe three possibilities.

(I) We could look for increased accuracy.

(a) We could, for example, find a specific form of $f(P)$ in the equation

$$\frac{1}{P}\frac{dP}{dt} = f(P)$$

by fitting a curve to a plot of $(P_{n+1} - P_n)/P_n$ against P_{n+1}.

Such a procedure may be appropriate if working with a particular population, but it sacrifices generality.

(b) We could increase accuracy without sacrificing generality by complicating the model a bit by adding an extra parameter. Thus we could 'generalise' the logistic to

$$\frac{dP}{dt} = P(1 - P/M)^\alpha \quad (\alpha \text{ a positive real number})$$

and work with this.

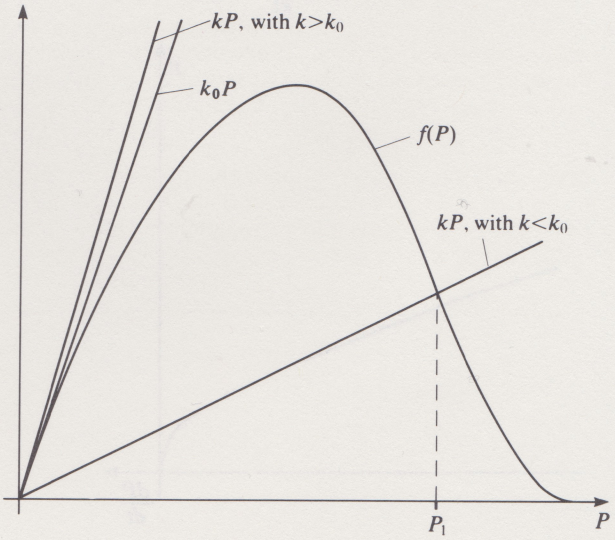
(II) We could try to analyse the real situation further, either in general or for a particular population, by taking more details of the biology into account. For example, we could set up a model that took account of the age, and sex structure of the population.

(III) We could try to further increase the generality of the model by looking for a model that covers other types of population variation, such as the periodic variations of the Canadian lynx population. (We might expect a time-delay model to do this.)

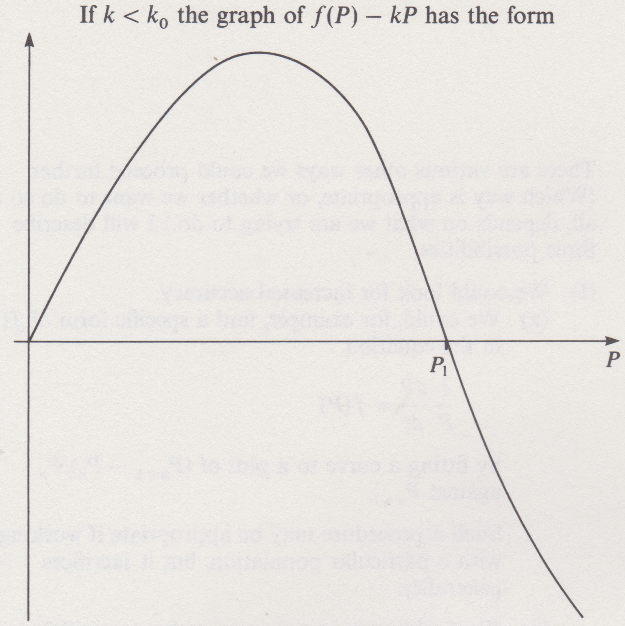
Solution to the problem in Section 4

1. Bearing the last part of the problem in mind I will investigate the qualitative nature of the solutions in the general case, when the behaviour of the unexploited population is given by $\frac{dP}{dt} = f(P)$, where $f(P)$ has the form shown in Figure 6. This will include Equation (3) as a special case. You should satisfy yourself that those steps of my argument which concern the *qualitative* nature of the solutions apply equally well if $f(P)$ is replaced by $aP\left(1 - \frac{P}{M}\right)$.

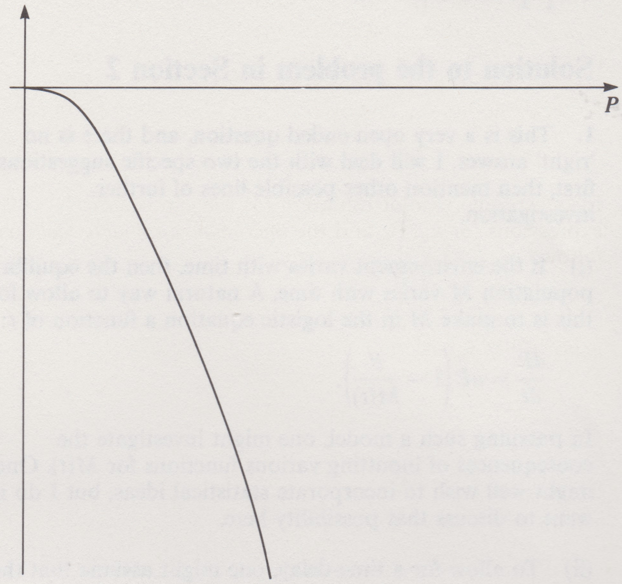
To draw a direction field for the differential equation $\frac{dP}{dt} = f(P) - kP$, I will first obtain sketch graphs of $f(P) - kP$ against P. The forms of the graphs depend on whether k is greater than or less than the number k_0, where k_0 is chosen to make the line k_0P tangential to the graph of $f(P)$ at $P = 0$ (i.e. $k_0 = f'(a)$).



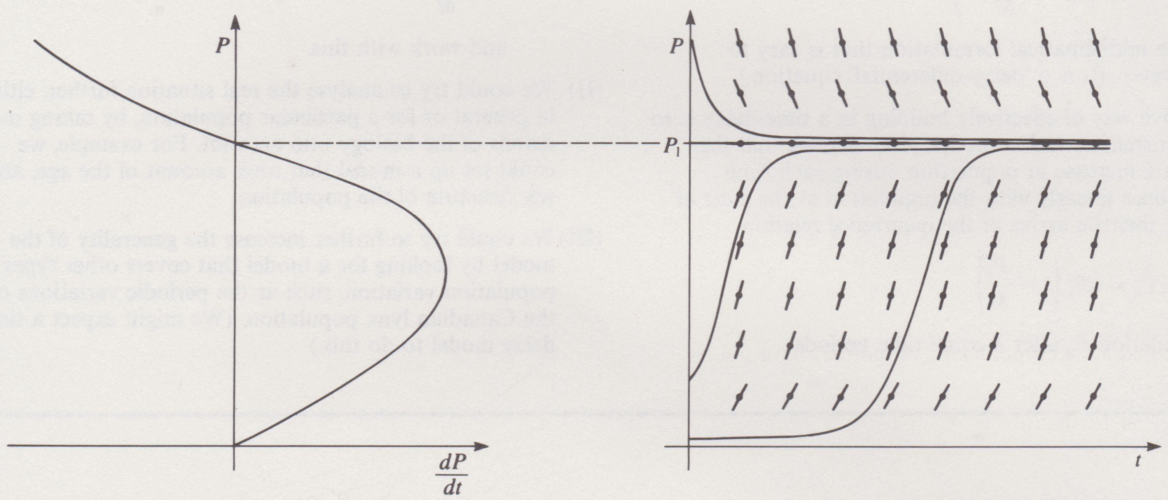
If $k < k_0$ the graph of $f(P) - kP$ has the form



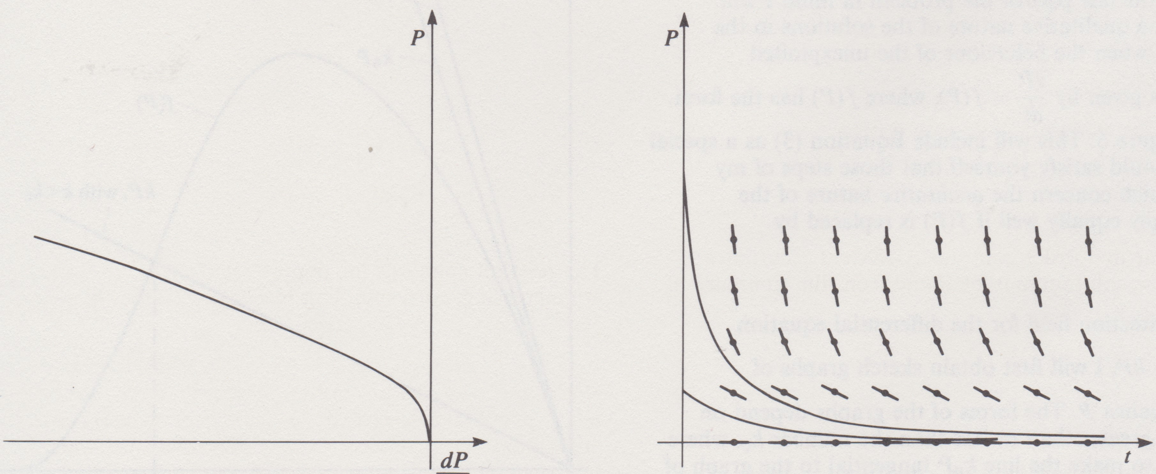
If $k > k_0$ the graph has the form



We can use these graphs to construct direction fields for the differential equation, as in the text of Subsection 4.1. The general shape of the solutions is not dependent on the particular form of $f(P)$, and so the solutions of Equation (3) are of the general form shown below.



Sketches of the solutions of $\dfrac{dP}{dt} = f(P) - kP$ for $k < k_0$, obtained using direction fields.



Sketches of the solutions of $\dfrac{dP}{dt} = f(P) - kP$ for $k \geq k_0$

The parameter k is the proportionate rate of catch; it can be used to measure the rate at which exploitation takes place. We see that if the exploitation rate is high ($k \geq k_0$) then the population is driven to extinction. If the exploitation rate is not too high ($k < k_0$), then the population remains viable under exploitation, whatever the initial conditions. In the long term the population will settle at a level P_1 dependent on the value of k.

In the specific case of Equation (3), we can obtain expressions for k_0, P_1 and the *maximum sutainable yield* as follows.

The long-term equilibrium P_1 will occur when $\dfrac{dP}{dt} = 0$ for the exploited population. That is, P_1 is a root of

$$aP\left(1 - \frac{P}{M}\right) - kP = 0.$$

The solutions of this are $P = 0$ and $P = \left(1 - \dfrac{k}{a}\right)M$. Thus

$$P_1 = \left(1 - \frac{k}{a}\right)M.$$

To find k_0, recall that the line k_0P is tangential to the graph of $aP\left(1 - \dfrac{P}{M}\right)$ at $P = 0$. So k_0 is equal to the derivative of $aP\left(1 - \dfrac{P}{M}\right)$ at $P = 0$, that is

$$k_0 = a.$$

The actual catch in this model is kP. Eventually this will reach equilibrium and settle at the sustainable yield $kP_1 = k\left(1 - \dfrac{k}{a}\right)M$. This expression is a quadratic in k, so its maximum value occurs midway between its roots. The roots are $k = 0$, and $k = a$, so the maximum sustainable yield occurs when $k = \dfrac{a}{2}$. (This result can also be obtained by calculus methods.) So

$$\text{Maximum sustainable yield} = \frac{a}{2}\left(1 - \frac{a/2}{a}\right)M = \frac{aM}{4}.$$

Note: this is the same expression as we obtained for the maximum sustainable yield in Exercise 1 using the 'constant catch' model (as one would expect).

These expressions for k_0, P_1 and maximum sustainable yield derive from the specific assumption that the growth of the unexploited population would be logistic. They are therefore less reliable than the qualitative results described earlier. However, note that the optimum exploitation rate ($k = a/2$) for Equation (3) occurs *well below* that causing extinction ($k = a$). This will remain true more generally.

Solutions to problems in Section 5

1. (i) Suppose that the population is P_n in the nth year (after a specified starting point). If we ignore migration we have

$$P_{n+1} - P_n = \text{Births in year } n - \text{Deaths in year } n = B_n - D_n, \text{ say.}$$

Now, from the assumptions given,

$$B_n = B$$
$$D_n = dP_n$$

where B and d are constants. Hence

$$P_{n+1} - P_n = B - dP_n. \qquad (1)$$

This is a suitable recurrence relation model.

(ii) We can rewrite Equation (1) as

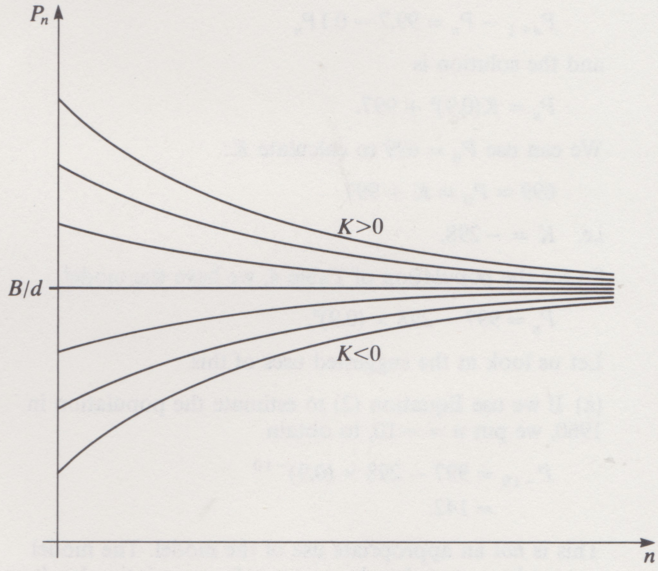
$$P_{n+1} = (1 - d)P_n + B.$$

This is a linear first-order constant coefficient recurrence relation, whose solution may be found from the summary of *Unit 1*, Section 1. It is

$$P_n = K(1 - d)^n + \frac{B}{d},$$

where K is a constant.

Since d is the *proportionate* death rate we must have $0 < d < 1$. So $0 < (1 - d) < 1$ and $(1 - d)^n$ tends to zero as n becomes large. A graph of the solutions is shown below.



The relevant solutions for population *growth* are those that are increasing, corresponding to negative values of K.

(iii) One would *not* expect this model to be appropriate for a population starting from a low level. A small population would not normally be able to generate the full number of births possible; this number would not be reached until the population had increased. (It is conceivable that if the environmental limit were itself low, then a low initial population could very rapidly grow to the level able to generate the maximum possible births. The wolves of Figure 2(b) of Section 1 are a possible example of this.)

For a population near its equilibrium value, the logistic equation will give similar results to the model in (i). The shape of the graphs suggests this, and it could be justified more formally, but I shall not do this.

(iv) The number of births each year is fairly steady. The mean number is 99.7 hundreds, and the figures given all fall within $\pm 5\%$ of this. So the first assumption seems reasonable. Of the 699 hundred birds present in 1970, $699 + 104 - 729 = 74$ must have died during 1970 (assuming there is no migration). The table shows the calculation of deaths and death rates.

Year n	Total population, P_n (hundreds)	Number of juveniles (hundreds)	Deaths in year n (hundreds)	Deaths as a proportion of P_n
1970	699	99	74	10.6%
1971	729	104	72	9.9%
1972	758	101	74	9.8%
1973	780	96	82	10.5%
1974	800	102	73	9.1%
1975	824	97	83	10.1%
1976	840	99	—	—

The mean death rate is 10% each year. The actual rates vary from 9.1% to 10.6%, but the assumption that the death rate is, on average, constant seems tenable. (Particularly as this is a biologically reasonable assumption, in appropriate circumstances, which I will assume hold here!) So the second assumption also seems reasonable.

If we denote by P_n the population in hundreds n years after 1970, the model of part (i) becomes, for this population (taking $B = 99.7$ and $d = 0.1$)

$$P_{n+1} - P_n = 99.7 - 0.1P_n$$

and the solution is

$$P_n = K(0.9)^n + 997.$$

We can use $P_0 = 699$ to calculate K:

$$699 = P_0 = K + 997$$

i.e. $K = -298$.

So for the population of Table 4, we have the model

$$P_n = 997 - 298 \times (0.9)^n. \qquad (2)$$

Let us look at the suggested uses of this.

(a) If we use Equation (2) to estimate the population in 1960, we put $n = -10$, to obtain

$$P_{-10} = 997 - 298 \times (0.9)^{-10}$$
$$= 142.$$

This is *not* an appropriate use of the model. The model cannot be expected to be accurate for population levels well below the equilibrium level—and 14 200 is well below equilibrium, and so outside the range in which the model is valid.

(b) Putting $n = 20$ in Equation (2) gives

$$P_{20} = 997 - 298 \times (0.9)^{20}$$
$$= 961.$$

So the model predicts a population of 96 100 in 1990. Assuming that environmental conditions do not change (a hazardous assumption!), this is a reasonable use of the model.

(c) The model implies an equilibrium population of 99 700 or, to a more sensible degree of accuracy, 100 000. To say that under present environmental conditions this is the equilibrium level of the population is an eminently reasonable use of the model.

(d) The model will be within 5% of equilibrium when $P_n = 0.95 \times 997$. This occurs when

$$0.95 \times 997 = 997 - 298 \times (0.9)^n$$

giving

$$(0.9)^n = \frac{997 \times 0.05}{298}$$

so

$$n = \frac{\log_e\left(\dfrac{997 \times 0.05}{298}\right)}{\log_e(0.9)} = 17.$$

Assuming environmental conditions do not change it is not unreasonable to say that the model implies that the population will by 1987 be within 5% of its equilibrium value. Given the accuracy with which the model fits the data, one must certainly regard the population as having 'effectively reached equilibrium' if it is within 5%.

(e) There is no point in looking at this model with a microscope.

2. I will model the exploitation as occurring continuously (rather than in discrete occurrences every three weeks, as it actually does). If the catch rate is C grams per 3 weeks, and C is K% of P (the population in grams), then

$$C = \frac{K}{100}P.$$

The data suggests that for each constant rate of exploitation K the population reaches an equilibrium level P_E. When this happens there is a sustainable yield Y grams per three weeks given by

$$Y = \frac{K}{100}P_E.$$

Before I can find the exploitation rate K that maximizes this sustainable yield I will need to find a relationship between P_E and K.

I will assume provisionally that the unexploited population would grow logistically:

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right).$$

So the exploited population changes according to the differential equation

$$\frac{dP}{dt} = aP\left(1 - \frac{P}{M}\right) - \frac{KP}{100}.$$

Now if the population is stable $\dfrac{dP}{dt} = 0$, so the equilibrium population P_E is given by

$$\frac{K}{100}P_E = aP_E\left(1 - \frac{P_E}{M}\right).$$

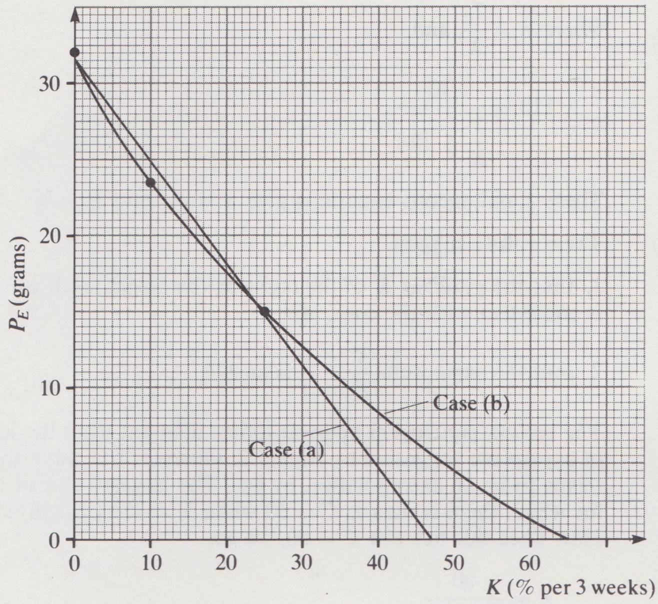
We are not interested in $P_E = 0$, so

$$\frac{K}{100} = a\left(1 - \frac{P_E}{M}\right),$$

or

$$P_E = M\left(1 - \frac{K}{100a}\right).$$

Thus the assumption that the unexploited population grows according to the logistic equation implies that P_E declines linearly with K. There isn't much data to support this, but what there is is shown below. I've drawn in a straight line fit to the three data points.



The straight line fit can be seen to imply that exploitation rates above about 46% will drive the population to extinction. Now it is clear from Figure 1(b) that an exploitation rate of 75% drives the population to extinction, but it is not clear whether extinction occurs at 50% exploitation, or whether there is equilibrium at a low population level (below 5 grams). The straight line probably shows P_E declining too rapidly with increasing K, suggesting that the population deviates slightly from the logistic model and that we should look for a non-linear relationship between P_E and K.

In the diagram I have also drawn (by eye) a smooth curve through the three data points. The curve implies an equilibrium population of about 4.5 grams at 50% exploitation, and extinction occuring at about 65% exploitation. This is not inconsistent with the data.

The straight line represents a 'pessimistic' assumption about the rate at which P_E declines with K, the curve an 'optimistic' assumption. I will investigate the implications of both assumptions for maximum sustainable yield, and the appropriate exploitation rate.

Recall that the sustainable yield Y at exploitation rate K % is given by

$$Y = \frac{KP_E}{100}$$

(a) *Assuming the graph of P_E against K is linear*
In this case P_E is a linear function of K and so Y is a quadratic function of K. The maximum sustainable yield will occur midway between the roots of the quadratic. These roots are $K = 0$, and (from the straight line on the graph) $K = 47$. So the maximum sustainable yield occurs at an exploitation rate of 23.5%.

From the graph, P_E is then 15.7 and so the maximum sustainable yield is

$$\frac{23.5 \times 15.7}{100} = 3.69 \text{ grams per three weeks.}$$

(You will need a larger copy of the graph than that reproduced above to be able to read values to the accuracy quoted in this solution.)

(b) *Assuming the graph of P_E against K is the curve shown*
In this case, as we do not have an equation for the curve, we must find the maximum yield by examining the values of $KP_E/100$ found from reading the graph. The values I obtained are shown below.

K	P_E	$KP_E/100$
10	23.5	2.35
20	18	3.6
25	15	3.75
30	12.5	3.75
29	13	3.77
28	13.5	3.78
27	14	3.78
26	14.5	3.77

In this case the maximum sustainable yield is about 3.78 grams per three weeks and occurs at an exploitation rate of 27–28%.

The conclusions from our two different assumptions are quite similar. This is encouraging: we can be much more confident that our conclusions are appropriate if they are not sensitive to likely variations in the assumptions on which they are based.

I will now look at the consequences of basing my recommendation on the wrong assumption. Suppose I pursue the recommendation $K = 23.5$ (based on Assumption (a)), if in fact (b) is correct. The equilibrium population P_E corresponding to $K = 23.5$ would (from the curved graph of Assumption (b)) be 15.9 and so the consequent yield would be

$$\frac{23.5}{100} \times 15.9 = 3.74 \text{ grams per three weeks}$$

—marginally lower than the maximum of 3.78 grams per three weeks obtainable if Assumption (b) were correct. Looking at the reverse case, I shall consider the recommendation $K = 27$ (based on Assumption (b)), if in fact Assumption (a) is correct. The equilibrium population P_E corresponding to $K = 27$ would (from the straight line graph of Assumption (a)) be 13.2 giving a consequent yield of

$$\frac{27}{100} \times 13.2 = 3.56 \text{ grams per three weeks}$$

—a slightly more substantial reduction below the maximum of 3.69 grams per three weeks obtainable if Assumption (a) were correct.

Although Assumption (b) is perhaps more likely to be correct (suggesting an exploitation rate of 27%) the consequences of recommending an exploitation rate of slightly *lower* than 27% are marginal even if Assumption (b) is correct. If Assumption (a) is correct and exploitation is at 27%, the result is a small but significant reduction in the yield obtained. Hence if this were a practical fishery I would recommend an exploitation rate lower than 27%. Since we actually have data showing that a yield of $\frac{25}{100} \times 15 = 3.75$ grams per three weeks can be obtained at an exploitation rate of 25% per three weeks, this is the rate I would recommend.

3. (i) We would expect that, for a particular trawler, the catch would be proportional to the number of hours actually fishing (for a fixed fish density). So the second measure of 'fishing effort' looks preferable.

(ii) (a) The total time T is the sum of the fixed time T_0 and the variable time T_1:

$$T = T_0 + T_1 \qquad \text{(all in days)}.$$

If C = catch rate per hour actually fishing, then the total catch X is given by

$$24CT_1 = X \qquad (1)$$

(assuming a constant catch rate during each trip). If the catch per day at sea is Y, then

$$Y = \frac{X}{T_0 + T_1} = \frac{X}{T_0 + (X/24C)} = \frac{C}{\frac{1}{24} + (T_0/X)C}. \qquad (2)$$

(b) The graph of Y against C for Equation (2) is a curve whose slope at $C = 0$ is 24 [check by differentiation], and whose slope gradually decreases as C increases. The curve increases to a limit at $Y = \dfrac{X}{T_0}$.

Figure 2 shows a curve of decreasing slope, which can be expected to have a horizontal asymptote (satisfactory).

The gradient of Figure 2 near the origin seems to be about 5. This is too far from the prediction of the model to be satisfactory.

However the nature of the discrepancy suggests how the model may be modified to remove it. If the term $\frac{1}{24}$ were $\frac{1}{5}$ (say), then the model could fit. The term '24' appears in Equation (1) because days have 24 hours—which they do, don't they? However, thinking back to the real situation, this discrepancy reminds me that I have assumed in Equation (1) that when boats are actively fishing, they fish for 24 hours a day. Put like this, this looks unlikely. It could be that 5 hours a day actually fishing is more realistic. I will modify my model, by assuming that when boats are on the fishing grounds, they fish K hours per day, on average.

This changes Equation (1) to

$$KCT_1 = X$$

and so Equation (2) becomes

$$Y = \frac{C}{\frac{1}{K} + (T_0/X)C}$$

(c) Yes. We get

$$50 = \frac{10}{\frac{1}{K} + 10A}$$

where $A = \dfrac{T_0}{X}$, and

$$110 = \frac{30}{\frac{1}{K} + 30A}.$$

These simultaneous equations give $A = \frac{1}{275}$ and $K = \frac{55}{9}$.

These values suggest:

1. that the gradient K of the curve at the origin is $6\frac{1}{9}$, which is consistent with the data, and

2. that the asymptote $\dfrac{X}{T_0} = \dfrac{1}{A}$ is at 275.

The second conclusion appears rather different from the level of asymptote suggested by Figure 2. However the curve there seems to be an extrapolation by eye. The largest value of C for which there is data is $C = 60$ when $Y = 150$ (roughly). How does this fit? For $C = 60$, we get

$$Y = \frac{60}{\frac{9}{55} + \frac{60}{275}} = 151 \text{ (to 3 significant figures)}.$$

This is a reasonable fit.

(d) The implications of the model are consistent with the data, despite the implicit assumption that the ratio $\dfrac{X}{T_0}$ is the same for all trawlers for which data is given in Figure 2. If we assume the model is accurate we can conclude:

1. that trawlers in this fishery fish about 6 hours per day on average while they are on the fishing grounds, and

2. that (again on average) the ratio of hold capacity to fixed time per trip is 275 cwt/day, and this sets an upper limit to the catch per day at sea that boats can achieve during a trip.

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